The University of Chicago

THE EFFECT OF A CONTROLLED NITROGEN SUPPLY WITH DIFFERENT TEMPERATURES AND PHOTOPERIODS UPON THE DEVELOPMENT OF THE POTATO PLANT

A DISSERTATION SUBMITTED TO THE FACULTY OF THE DIVISION OF THE BIOLOGICAL SCIENCES IN CANDIDACY FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY
1934

By
HARVEY OSCAR WERNER

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CHICAGO, ILLINOIS

Reprinted from
Nebraska Agricultural Experiment Station
Research Bulletin 75, September, 1934

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SUMMARY

1. The purpose of this work was to study the effect of nitrogen upon the development and composition of the different parts of the potato plant when grown with various temperatures and photoperiods. The plants were grown in sand, to which nutrient solutions were added.

2. With different temperatures and photoperiods the extent, rate, and place of N assimilation and carbohydrate synthesis and utilization were greatly altered. Consequently the nature and extent of the morphological responses of the plants to changes in the external N supply were altered to a comparable extent.

3. Carbohydrates accumulated (and tubers formed) whenever they were not utilized in the formation of new tissues or the maintenance of those previously formed (respiration). The inability of the plant to utilize carbohydrates in building new tissues resulted from an inhibition of the assimilation of N. This occurred at low temperatures or in short days or when N was withheld from the nutrient solution. Excessive respiration prevented carbohydrate accumulation or created a deficit when the temperature was high, especially if the days were long.

4. High temperatures, long days, and an abundant external supply of N favored vegetative growth (in all plant parts except tubers), whereas early tuberization was induced with low temperature, short days, or a deficiency of N. Maximum tuberization occurred with days of intermediate length, low temperature, and an abundant N supply.

With adequate N the most distinctive types of the plants were as follows:

(a) Small plants, with very high ratio of tubers to tops, produced when days were cool and short;

(b) Larger plants, having lower tuber/top ratios but producing the greatest weight of tubers, produced with intermediate day length and low temperatures;

(c) Still larger but less tuberous plants, produced as days became either longer or warmer;

(d) Less vigorous plants, devoid of tubers and sometimes of stolons, produced when temperatures were very high and days long.

When either day length or temperature, or both, was increased vegetative growth resulted, whereas tuber formation occurred as they were decreased. Tubers were produced at temperatures commonly considered too high for tuberization by withholding N from the nutrient solution, or at even still higher temperatures by use of a short (10½ hr.) photoperiod.

5. Withholding N from the nutrient solution when conditions were most favorable for maximum vegetative growth (long, warm days) resulted in a prompt and extensive decrease in the inorganic N in the plant, accompanied by retardation of vegetative growth, carbohydrate accumulation (especially starch), and either prompt initiation or acceleration of tuber development. As the N deficiency was prolonged, accumulated starch disappeared from leaves and stems, leaves became pale, maturity was hastened, and final total weight of tubers was materially reduced. When conditions were favorable for maximum tuber development but least favorable for vegetative growth, withholding N did not measurably accelerate tuberization but it inhibited vegetative growth and lowered final tuber yield.

6. Resupplying N to N-starved plants resulted in a rapid increase of inorganic N in all plant parts, a rapid reestablishment of the chlor-

ophyll supply, and rapid synthesis of N compounds. With long days vegetative growth was resumed, causing immediate retardation but later acceleration of tuber growth rate. With short days, vegetative growth was not resumed. Under all conditions the life of plants was prolonged and tuber yields were generally increased.

7. Maximum stolon growth, *i.e.*, long primary stolons and numerous and long lateral and branch stolons, occurred when conditions were especially favorable for vegetative growth. Under conditions most favorable for vegetative growth, stolon axes (except those terminated by tubers) continued to be initiated or elongated after tubers had formed on primary stolons, whereas under conditions most favorable for tuberization practically all stolon growth ceased when the first tubers developed.

8. In rapidly growing plants the percentage of dry matter decreased from leaves to petioles, upper and lower stems, and to the stolons, and then increased in the tubers to the highest percentage. The highest percentage in tubers occurred when conditions were very favorable for accumulation of carbohydrates, *i.e.*, short days, low temperatures, and when the N supply was deficient.

9. Whenever or wherever N was being assimilated into the plant structure, the percentage of inorganic N was low. Consequently it was lowest in tubers, followed by leaves and highest in the stems, and was low in all parts when days were long and temperature high, or when N was withheld from the nutrient solution.

10. The highest percentage of assimilated or organic N occurred in the leaves, next highest in the tubers, and lowest in the stems. In young plants most of the assimilated N (fresh-weight basis) was found in the leaves, but as tubers developed a constantly increasing percentage of the assimilated N in the plants was found in the tubers. The amount of organic N in tubers continued to increase till plants were mature, even though it decreased in the vegetative parts late in the life of the plant.

11. Plants that were tuberizing rapidly and were not producing vegetative portions had only a slightly higher percentage of total hydrolyzable polysaccharides in leaves and tubers than did plants that continued to be distinctly vegetative. Tuber-producing plants generally had a higher percentage of sucrose but a lower reducing-sugar content than the more vegetative plants.

The Effect of a Controlled Nitrogen Supply with Different Temperatures and Photoperiods upon the Development of the Potato Plant

H. O. WERNER[1]

The potato (*Solanum tuberosum*, Linn.) is grown under a great variety of conditions with regard to temperature, length of day, intensity and character of light, texture, fertility, and moisture of soil, and atmospheric humidity. There is need for a better understanding concerning the internal response of the potato plant to these external conditions when they are applied, either singly or in combination with each other, and the resulting morphological response, especially with regard to the tuberization process.

The basic physiological principles underlying the extent and time of development of vegetative and reproductive organs have been established chiefly through a series of investigations by Fischer (*39*)[2] Klebs (*55-58*), and Kraus and Kraybill (*64*). The potato tuber is a vegetative organ greatly modified for storage purposes and used for reproductive purposes. In this connection it is well to keep in mind that "vegetative development" and "fruiting" or "tuberization" are not opposite or antagonistic processes but that, as others have stated, "each is an external expression of an internal condition" (*64*).

Garner and Allard (*41*) have advanced the idea that tuber-producing plants vary through a series of physiological stages ranging from extreme vegetative growth, through flower and fruit formation to tuber production.

The significance of temperature in the tuberization process was conclusively demonstrated by Bushnell (*18*) in 1925. Garner and Allard (*41*) pointed out the importance of length of day in relation to tuber development. Since then a large number of workers have verified their results and have made important contributions concerning the photoperiodic response of different varieties and the effect of photoperiods of varying length as influenced by different temperatures and the carbon-dioxide content of the atmosphere.[3] The ef-

[1] The macrochemical analyses were made under the general supervision of the author by Mr. G. R. Astleford in the laboratory of the Department of Agricultural Chemistry. The author also wishes to acknowledge the coöperation of Mr. Chas. McCoy, who attended to much of the detail work involved in growing the plants. In planning the work the author received numerous valuable suggestions from Dr. E. J. Kraus and Dr. C. E. Shull of the University of Chicago and Dr. G. T. Nightingale of the New Jersey Agricultural Experiment Station.

[2] Italicized numbers in parentheses refer to literature cited on pp. 126-132; parenthetical numbers not italicized refer to experimental treatments.

[3] Pertinent literature concerning various aspects is reviewed in the opening portions of the various sections of this bulletin.

fect of soil moisture and fertility upon yield of tubers has been studied in a large number of field-plot experiments and in addition the nutrient requirements have been quite thoroughly investigated with water and sand cultures, particularly by German and American workers. The relation of each of the important chemical elements to the fundamental process of tuberization represents a relatively undeveloped field of investigation.

It has been the object of this investigation to determine the relation of the nitrogen supply to the processes of stolon and tuber formation with different temperatures and with photoperiods of different lengths, and at the same time to determine some of the internal physiological responses accompanying these morphological responses.

EXPERIMENTAL METHODS

LIGHT AND TEMPERATURE

Experimental series of identical plan were run in the greenhouse at different times from June, 1932, to August, 1933. The different series and conditions under which they were grown were as follows:

Series A.—June to September, 1932. Long days decreasing in length and high temperatures also decreasing.

Series B.—October, 1932, to January, 1933. Short days decreasing in length and low temperatures also decreasing slightly.

Series C.—February to April, 1933. Short days increasing to medium length and temperatures constantly low.

Series D.—April to June, 1933. Long to very long days and high to very high temperatures.

Series DS.—Short-day plants receiving 10.5 hours of daylight from 7:15 A. M. to 5:45 P. M. each day (secured by covering plants with knock-down light-tight ventilated chambers). Season and temperature same as Series D.

Series E and ES.—Comparable to D and DS but grown from July to September, 1933, with long days and 10.5-hour days at high temperature.

Series X.—A supplemental series in which inorganic nitrogen was added to or withheld from the nutrient solution at intervals beginning with planting time.

The exact dates for each series except X as well as day lengths, mean temperatures, light intensity, etc., for various periods are summarized in Table 1 and data on daily temperature and lengths of day are graphically presented in Figure 1.

VARIATION IN THE SUPPLY OF NITROGEN SALTS

In each of the previously enumerated series nitrogen salts were supplied in or withheld from the nutrient solution supplied to groups of plants during the four major periods, which were arbitrarily established as follows:

Period 1.—From planting time and continuing during the stolon-developing period but terminating just as tubers were beginning to develop.

Period 2.—The period of tuber setting and early expansion when greatest vegetative growth occurred.

Period 3.—The period of most rapid tuber growth, during which the vegetative growth rate was greatly reduced.

Period 4.—Period of maturity, during which practically no vegetative growth occurred or tops were actually dying but tubers were still increasing in weight, the rate depending upon effect of light and temperature.

The following tabulation shows the nitrogen treatments by periods and the time of harvesting each lot.

Lot numbers—all series	First period	Second period	Third period	Fourth period	Harvested at end of period
1	Nitrogen	.....	.....	.....	1
2	Nitrogen	Nitrogen	.....	.....	2
3	Nitrogen	Nitrogen	Nitrogen	.....	3
3′	Nitrogen	Nitrogen	Nitrogen	Nitrogen	4
4	Nitrogen	Nitrogen	None	.....	3
4′	Nitrogen	Nitrogen	None	None	4
5	Nitrogen	None	.....	.....	2
6	Nitrogen	None	Nitrogen	.....	3
6′	Nitrogen	None	Nitrogen	Nitrogen	4
7	Nitrogen	None	None	.....	3
7′	Nitrogen	None	None	None	4

This scheme of treatments is shown semi-diagramatically on page 16.

GENERAL PROCEDURE IN GROWING THE EXPERIMENTAL PLANTS

Dormant seed potatoes of Nebraska No. 22 Triumph, a tuber line of medium earliness, were disinfected with corrosive sublimate for protection against Rhizoctonia (*Corticium vagum*, B. and C.) and were then cut into uniform seed pieces (15 grams each). These were planted in river sand to sprout. Seed pieces with sprouts about one inch long (all except one sprout per seed piece removed) and with roots several inches long, were planted in sand, in 10-inch (25.5 cm.) clay pots, one plant per pot, with the top of the seed pieces uniformly 10 cm. below the tops of the pots and each piece covered with about 8 cm. of sand. River sand, after being screened through a ⅛-inch-mesh screen, was washed thoroughly and then sterilized in the pots with live steam at 20-25 pounds pressure for three hours.

In order to avoid inequalities of illumination and temperature the plants of each treatment were systematically distributed in the two 24-foot-long sections of a 25-foot-wide wooden rafter greenhouse running north and south. Both sections were shaded by another house in the morning but

TABLE 1.—*History of the experiments.*

Factor	Period	Series A, high temp., long day, decreasing	Series B, low temp., short day, decreasing	Series C, low temp., short to medium day	Series D,[1] high temp., long to very long day	Series E,[1] high temp., long day, increasing
Date into sand		June 18	Oct. 11	Dec. 27	Apr. 16	June 27
Date into pots		July 1	Oct. 19	Jan. 19	Apr. 26	July 7
Modal emergence date		July 3	Oct. 26	Jan. 31	Apr. 30	July 11
Date harvested and number days after emergence when each period was terminated	First	July 25	Nov. 11	Feb. 18	May 15	July 29
		22	16	18	15	18
	Second	Aug. 22-23	Dec. 2-3	Mar. 10-11	May 30	Aug. 21
		50-51	37-38	38-39	30	41
	Third	Sept. 10	Dec. 22	Mar. 31	June 8-9	Aug. 31
		69	57	59-60	39-40	51
	Fourth	Sept. 24	Jan 13.	Apr. 13-14	June 12	Aug. 31
		83	79	72-73	43	51
Range of temperature and daily mean during each period, degrees F.	First	57-112	59-88	47-68	56-93	60-115
		86.4	70.0	60.5	72.3	81.0
	Second	58-102	52-74	54-72	53-105	60-98
		80.0	62.3	60.1	73.9	84
	Third	55-100	48-72	50-76	65-102	60-85
		78.9	59.5	61.8	92.1	76.0
	Fourth	53-100	54-86	54-79	66-120	.....
		76.2	62.0	64.3	85.1	.....
Day length on first and last day of each period, hours, minutes	First	15-4	10-40	10-4	13-55	14-56
		14-36	10-15	10-47	14-29	14-27
	Second	14-35	10-13	10-51	14-24	14-27
		13-35	9-25	11-43	14-54	13-35
	Third	13-31	9-24	11-44	14-56	13-35
		12-43	9-13	12-38	15-3	13-9
	Fourth	12-42	9-14	12-38	15-3	.....
		12-3	9-30	13-15	15-5	.....
Radiation outside of greenhouse as mean gram calories per day and per hour of daylight	First	600.8	228.5	302.7	340.0	.....
		40.8	21.3	29.0	24.0	.....
	Second	471.0	201.8	372.1	634.0	.....
		33.6	20.6	31.4	43.4	.....
	Third	464.0	189.6	384.2	649.5	.....
		35.4	17.5	31.8	43.4	.....
	Fourth	417.5	194.0	432.0	683.0	.....
		33.7	18.2	33.8	45.2	.....
Date solutions changed from	1 to 5	July 26	Nov. 12	Feb. 20	May 11	July 29
	2 to 4, 5 to 6	Aug. 24	Dec. 31	Mar. 11	June 1	Aug. 18
Number of plants in samples harvested	First	16	17	32	12	4
	Second	6	10	9	8	4
	Third	8	6	9	9	4
	Fourth	6	6	6	6	..

[1]DS and ES grown with 10.5-hour day, otherwise same as D and E.

not in the afternoon. The increased space provided by the removal of plants at intervals eliminated practically all shading by the plants themselves as they became older.

Plants grown during any particular period of any one series or harvested at the end of that period are designated by the set and series number; for example 3C designates the plants receiving a complete nitrogen solution continuously that were grown during or harvested at the end of the third period of Series C.

A set of plants was harvested at the end of each period from each treatment and the proper solution changes were

made on the same day or within the next day or two (see Table 1).

ATMOSPHERIC CONDITIONS DURING THE EXPERIMENTS

During the summer and late spring (Series A, D) the temperature was rather variable, as the only means of altering it to any extent was by manipulating ventilators. During the fall, winter, and early spring (B, C) the temperature was thermostatically controlled. The variation through the 24-hour periods was seldom over 4 degrees F. (except for a few hours in the middle of the day when the temperature may have risen) as shown in Figure 1.

The data on light intensity were secured from the local radiation station operated by the Weather Bureau of the U. S. Department of Agriculture at a distance of less than a half mile from the greenhouses. These data are published in the Nebraska section of the monthly report of climatological data by the U. S. Weather Bureau. Tysdal (*123*) reports that four layers of glass of the thickness used cut out 55.8 per cent of the solar radiation as measured by a pyrheliometer when placed at an angle of 45°. Allowing for variation in the sun angle, he figured that the light intensity was reduced 64.45 per cent. He found (personally reported, not published) that one thickness of glass at an angle reduced the light intensity almost exactly one-fourth as much, or 16.1 per cent. When allowance is made for glass overlapping (about two inches in these houses) and dust and dirt on glass, shade of rafters, etc., the intensity would easily be reduced 20 to 25 per cent by one thickness of glass.

The maximum and minimum air temperatures as recorded each day by thermographs are shown in Figure 1. The daily means and period means were secured from these maxima and minima. The temperatures during the night and all except the middle hours of the day were relatively constant with Series B and C. The daily means thus derived tend to be too high, because the higher temperatures prevailed for only a few hours when the sun was shining brightly.

The temperature to which the roots and tubers were exposed was not the same as that of the air. Evaporation of water from the surface of the sand and through the pots lowered the temperature of the sand at night and during the daytime except when the sunshine was bright. Long-tube thermometers registered temperatures from 2 to 14 degrees F. lower in the center of the pot than air temperatures in the early morning—the difference depending upon the atmospheric humidity. In fact, when the sun was not shining

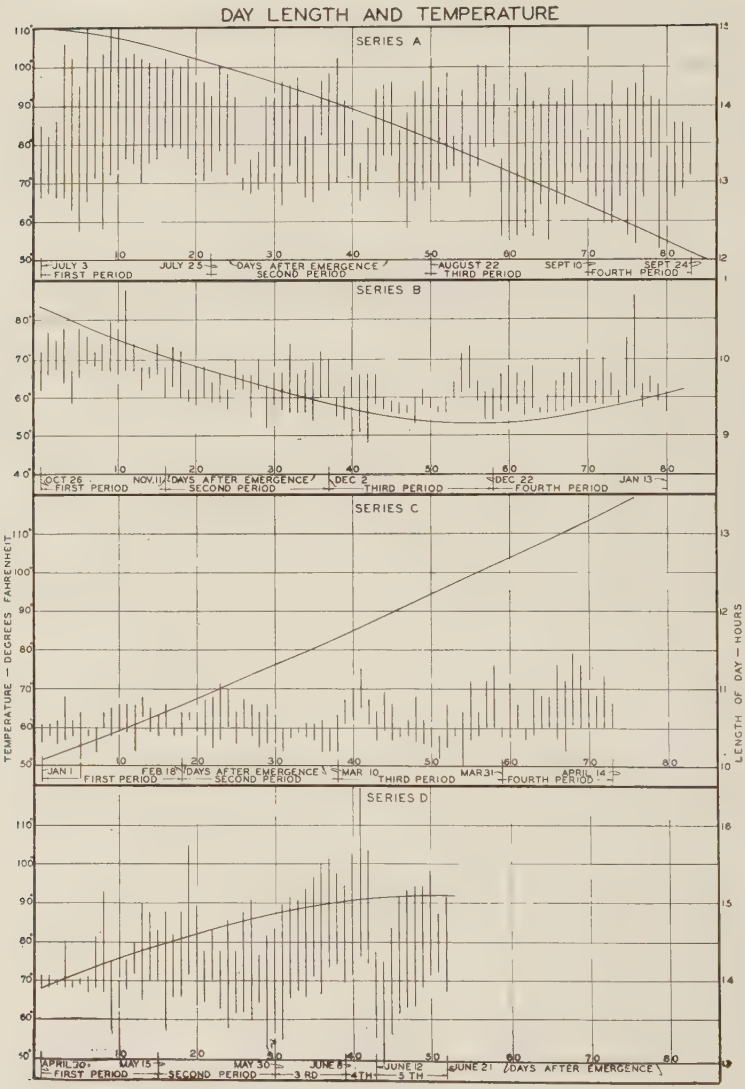


FIG. 1.—Range of temperature during each day and length of day from sunrise to sunset, for each day when the plants of the various experimental series were being grown.

and the air temperature had been constant for some time the temperature in the center of the pot was always within one degree of that of the wet bulb of the s ing psychrometer. When the sun was shining brightly the midday temperature

in the sand was commonly 8 or 9 degrees higher and frequently 16 to 18 degrees higher than the air temperature. Thus the temperature in the sand varied more than the air temperature and the daily mean was lower on almost every day.

To reduce evaporation to the minimum, the humidity was raised by sprinkling the walks and keeping the ground under the benches wet all the time.

NUTRIENT SOLUTIONS

The external nitrogen supply of the plants was altered by supplying, during definite periods, either a complete nutrient solution or a solution complete except for nitrogen.[4]

After a study of the results of dozens of workers with nutrient solutions of various compositions and concentrations as reported principally by Tottingham (*120*), Martin and Shive (*78*), Newton (*88*), Johnston (*52*), and Schropp and Zoller (*105*), it was deemed most desirable to use the three-salt solution designated by the type number R_2 S_1 (see Table 2). In view of the good results secured in the field with

TABLE 2.—*Composition of nutrient solution as partial-volume molecular concentrations of salts used.*

Character of solution	Series with which used	Treatment number with which used	Salts used				
			KH_2PO_4	$Ca(NO_3)_2$	$(NH_4)_2SO_4$	$MgSO_4$	$CaCl_2$
Complete, plus N	A, B	1, 2, 3, 3′, 6, 6′	.0045	.0090	.....	.0045	.....
Complete, plus N	C, D, DS, E, ES	1, 2, 3, 3′, 6, 6′	.0045	.0060	.0030	.0045	.....
Minus N	All	5, 4, 4′, 7, 7′	.0045	.....	.....	.0045	.0090

ammonium fertilizers with potatoes (*17*, *82*) and the desirable results secured with its use with the closely related tomato (*115*), the solution was modified to a four-salt solution when one-half of the nitrogen was supplied in the form of ammonium sulphate beginning with Series C. When Series B was being grown there was some concern as to whether the plants were assimilating nitrogen from the calcium nitrate. When nitrogen was omitted, calcium chloride was used at the same molecular concentration.

Immediately after planting, enough plus-N nutrient solution was applied to the surface of the sand to bring the level of the solution to a height of about 5 cm. in the graniteware

[4] For the sake of brevity the term "nitrogen" is used instead of longer statements, such as "nitrate nitrogen" or "ammonium nitrogen."

basins into which the pots were set. During periods of rapid growth, when temperatures were high and days long or bright, each of the plants received 1 litre of solution every day; when temperatures were low and days short or cloudy 1 litre of solution was applied two or three times per week to each pot. When the level of the solution in the pans became low between periods of nutrient application, water (acidulated tap water) was added directly into the basins.

At intervals of ten days or two weeks the pots were set out of the basins and were flushed with five litres of acidulated water, after which they were set back into the basins and again supplied with the requisite nutrient solution to the customary level. This system of flushing was even more thorough whenever a change was made from plus-N to minus-N solutions.

Tap water with a pH of about 6.8 was used. It contained a very little nitrogen but not enough to warrant the expense of using distilled water. Tiedjens and Robbins (*115*) have reported reduced assimilation of nitrogen from nitrates with a high pH in the rooting medium. Clark and Shive (*21a*) have reported that with the tomato the rate of absorption of nitrate N was greatest at a low pH (*i.e.* at 4) and of ammonium N at a high pH (at 7) when plants were 38 to 41 days old, but that when plants were 52 days old the pH exerted this dominating influence on nitrate absorption to a lesser degree. As plants became older the rate of ammonium N absorption decreased, while that of nitrate N increased. This tap water, when used either for flushing the pots or for diluting nutrients, was acidulated with commercial concentrated HCl.

These acidulated solutions which had a pH of 3.8 to 4.0, when applied to the sand containing roots of growing plants appeared in the drainage solution with a pH of 6.1 to 6.2 fifteen minutes later (chlorophenol red indicator), 6.6 to 6.8 eighteen hours later (bromthymol blue indicator), and 7.1 to 7.6 forty hours later (phenol red indicator). These pH values were possibly too high for ideal assimilation of nitrates. Tiedjens and Robbins (*115*) point out that these pH changes are greater with old than with young plants and they as well as Pirschle (*97*) point out that these changes are not so important with ammonia as with nitrate nutrients. Since this work was conducted, the balancing of ammonia and nitrate sources of nitrogen has been recommended as a method for maintaining a constant pH in nutrient solutions used for growing plants (*121*). This same method might be applicable in sand-culture work.

Iron was applied at the rate of one part per million of solution to Series A as ferric chloride and to Series B as ferric citrate, but because of doubt as to the effectiveness of these compounds in solutions used, on personal recommendation of Dr. Shive ferrous sulphate was used for the other series. Even though iron may at times have been inadequate, there were never any indications of iron-deficiency chlorosis, for probably the plants got some iron from the water and iron supports.

METHOD OF HARVESTING PLANTS

Because of the rapid carbohydrate changes that occur in plants from hour to hour as light and temperature vary and as photosynthetic material accumulates or is translocated, a means of harvesting was used which as nearly as was physically possible exposed plants of all sets of a series to the same range of conditions and enabled all of them to be put into the oven for drying at practically the same time. Harvesting was done from noon on, during bright, sunny days. One plant from each set of the series was brought to the laboratory and set on a wide sill of a window facing east. The plant was cut off at the surface of the sand and weighed at once; then the leaflets were stripped off the midribs and weighed separately, as were the remaining midribs, petioles, and stems. Both divisions were cut up at once, weighed again, and all put into the oven. While this was being done the corresponding plant of the next series was cut off and weighed. By this system the plant tops were cut up and in the oven within 30 to 40 minutes after being taken out of the greenhouse. As soon as the tops of all plants had thus been disposed of, the underground parts were carefully washed out, so as to leave all stolons, tubers, and roots attached. The roots were trimmed off, and in all but Series A and B all sand was washed through a sieve so as to catch all small pieces of roots and then all roots were dried. A record was then secured as to the position and length of each stolon, and position, weight, and dimensions of each tuber either by actual measurements as in Series A and B, by careful drawing and weighing as in C, or by photographing as in D and DS. With Series A and B, harvesting of tubers was not always completed till about 24 hours after the tops were cut off, but in Series C, D, and DS all tuber records were secured during the half day on which they were harvested. Whenever plants are reported as being harvested on two days, half of the plants of each set were harvested on each day.

METHOD OF DRYING PLANT MATERIAL FOR ANALYSIS

Because of the uncertainty as to how soon samples could be analyzed, the alcohol preservation method was considered inadvisable. If material is improperly handled, carbohydrate changes occur in the course of drying, due to respiration and hydrolysis. Numerous investigations (reported in *69, 71*) appear to show: that at high temperatures (98°C.) in succulent tissues much of the starch is hydrolyzed to sucrose (*138*) ; and at 45° C. sucrose is synthesized and with respiration a decrease in reducing sugars results. Link and Schulz (*70*) found that total nitrogen was not altered by any method of drying. Their work and some referred to by them showed no loss of inorganic nitrogen by drying. Sessions (*107*) was able to determine the inorganic nitrogen content in dried plant material to a very high degree of accuracy. At a later date Sessions stated that there is no change in nitrate content during drying if minced tissue is held at a temperature of 110° C. until most of the water is lost and the drying is then completed at 75°-80° C.[5] Nightingale (*89*) found no experimentally significant difference in nitrate content of stems of tomatoes when analyses were made of fresh material or of stems dried rapidly at 75° or 80° C. It was essential in this investigation to differentiate between organic and inorganic nitrogen, but as splitting of these into fractions was not desired, drying at reasonably high temperature appeared to be a satisfactory method.

The method adopted was to cut leaves into bits about 5 mm. square, and the stems into pieces not over 5 or 6 mm. in any direction. Tubers were cut into rectangles about 3 or 4 mm. square with the periderm on one side severed at only a few places. This permitted the spreading out of the pieces of tubers in fan-like style but prevented the loss of juice on the gauze, since the periderm side was placed on the screen. After the cut tuber surfaces were dried the larger groups of pieces were broken apart.

The material was dried on fine copper-gauze trays in a well-ventilated electric oven. When fresh material was being put into the oven the temperature in the lower part of the oven was maintained at 80°-85° C. and the upper part at 60°-70°. Freshly cut material was placed in the lower part of the oven and moved up as more recently cut material was added. After all material had been in the oven for two or three hours, the temperature was reduced to 70°-75° in the bottom and 55°-60° C. in the top. Initial weight loss ap-

[5] Letter from A. C. Sessions, December 1, 1932.

peared to be as rapid as that reported by Rosa (*101*) from Boswell's work, who found a loss of about 90 per cent of the water from tomato leaves in the first hour. Drying was generally continued for two days, by which time most samples were less than 5 per cent moisture. The material was then removed and bottled for storage. Absolute dry-matter determinations were made at 103°-105° C. with small samples in weighing bottles. The entire stored sample was ground in a Wiley mill and passed through a millimeter-mesh sieve before analysis.

MACROCHEMICAL ANALYTICAL METHODS

Inorganic nitrogen was determined by the Sessions and Shive method (*108*) from a one-gram sample, the "ammonia" and nitrate fractions being determined separately on all but the samples from the third period of Series D and fourth period of all other series.

The organic nitrogen was determined by a slight modification of the Kjeldahl-Gunning method—A. O. A. C. pp. 18-20, 1930 (*2*)—from the residue left after inorganic nitrogen was extracted. Because of the 2.5 gms. of Devarda alloy, the 10 gms. of sodium carbonate and 6 gms. of sodium chloride used in extracting inorganic nitrogen, the copper sulphate and sodium sulphate were omitted and 50 cc. of sulphuric acid was used and digestion continued 2.5 to 3 hours.

Sugar solutions were prepared by the official A. O. A. C. method—(*2*) p. 281, No. 20 (1930)—with 2-gm. samples of tubers and 4-gm. samples of other plant parts. Reducing sugars were determined by using the cuprous oxide method—A. O. A. C. p. 379, No. 38 (1930)—up to point of filtration, from which point the volumetric method was used according to Peters (*95*). Sucrose was determined by following the A. O. A. C. method—p. 281, No. 22 (1930)—determining reducing sugars as previously stated.

Starch (including dextrin) was determined from the insoluble residue remaining after extraction for sugar as was done by Johnston and Dore (*53*). One-tenth gram of takadiastase was used for each gram of material in the original sample, and neutral lead acetate was used for clarification and sodium carbonate for deleading, as in the preparation of the original sugar solutions.

Acid-hydrolyzable polysaccharides other than starch and dextrin (so-called hemicellulose) were determined from the residue after starch was removed, as by Johnston and Dore (*53*), the specified amount of HCl being added plus an amount equivalent to the one gram of $CaCO_3$ used at the time

of the original extraction. Clarification and deleading were done as in the starch determinations.

The residue, after all soluble materials and acid-hydrolyzable polysaccharides had been removed, was determined by drying at 100° C. in a weighed crucible.

MICROCHEMICAL METHODS

Nitrate determinations were made on thin small sections with an abundance of diphenylamine (0.1 gm. diphenylamine in 10 cc. 75% H_2SO_4). The sections were allowed to dry for a few minutes so as to intensify the color by reducing the water content of the sections (*49*). Starch was determined by the customary iodine method, using a solution of 0.3 gm. I and 1.5 gm. KI in 100 cc. of distilled water.

METHOD OF REPORTING EXPERIMENTAL RESULTS

The results of the experiments are presented under two general divisions:

(1) The morphological responses of the plants with the results and discussion arranged so as to consider the response of each organ or plant part at intervals to: (a) the photoperiod and temperature, and (b) the nitrogen treatments under each of these sets of conditions.

(2) The physiological responses within the plant as determined by: (a) macrochemical analysis for organic and inorganic nitrogen and for carbohydrate fractions, and (b) microchemical studies of sections of plants for nitrates and starch.

A uniform order is used in presenting data in all tables, so that information concerning any one lot of potatoes always appears in the same relative position. The order is as follows:

Period	Number of nitrogen treatments			
First	1			
Second	2		5	
Third	3	4	6	7
Fourth	3′	4′	6′	7′

The nitrogen treatments during these periods were as follows:

Period	Nitrogen treatments			
First	+N			
Second	+N		–N	
Third	+N	–N	+N	–N
Fourth	+N	–N	+N	–N

By this system the reader need only remember that all tabular divergences to the left present data from plants with which nitrogen was either continued in the nutrient solution

(Lots 1, 2, 3) or where it was supplied after a period of starvation (6), whereas all divergences to the right present data from plants which were grown during that period without nitrogen in the nutrient solution (Lots 5, 7, 4). Continuation of the same nitrogen treatment during the fourth period is shown by placing the data directly under those from the same treatment during the third period. This same arrangement is used for some of the illustrations.

TABLE 3.—*Comparative development of various parts of the continual-nitrogen plants in each series (maximum development for any character in all series rated as 10).*

Series	A	B	C	D	DS	E	ES
Temperature	High	Low	Low	High	High	Very high	Very high
Day length	Long	Short	Medium	Long	Short	Long	Short
Size of tops	9	1	4	10	7	7	5
Flowers—number, size	9	0	1	10	1	6	1
Stems:							
Length main axis	3	1	4	10	7	8	5
Laterals:							
Number	9	1	2	10	5	6	3
Length	9	1	2	10	3	3	2
Internodes—length	7	1	2	10	6	6	4
Thickness	9	1	3	10	7	4	2
Woodiness	8	1	4	10	4	5	2
Pigmentation	2	10	6	1	3	1	1
Leaves:							
Number	10	1	3	9	6	6	4
Size	3	10	9	1	7	3	4
Stem angle [1]	9	1	4	10	7	8	6
Leaflets:							
Number	7	1	3	9	6	10	5
Size	4	10	9	1	7	2	3
Roundness	3	10	9	1	8	3	6
Rigidity	9	1	3	10	5	6	3
Thickness	9	1	3	10	7	6	4
Ratio—leaves to stems [2]	3	10	8	1	5	4	6
Stolons:							
Primary (No.)	10	7	10	5	6	1	6
Lateral (No.)	6	1	9	10	7	0	4
Branches (No.)	10	1	6	10	4	0	2
To surface (No.)	9	0	1	10	0	7	0
Total length	10	4	7	9	2	1	1
Thickness	8	1	5	10	9	3	9
Tubers:							
Early setting	4	10	9	5	9	0	9
Number	10	6	9	4	9	0	8
Size	5	6	10	1	2	0	2
Total weight	3	4	10	0.2	2	0	1
Ratio—tubers to tops [2]	1	10	7	0.1	1	0	3
Tuberization efficiency [3]	4	10	9	0.2	5	0	7
Percentage dry matter:							
Tops	8	1	3	10	5	..	..
Tubers	7	9+	10	5	4	0	6
Percentage assimilated nitrogen:							
Leaves	8	1	7	10	8	..	..
Stems	7	2	1	10	2	..	..
Tubers	1	9	10	4	2	..	..

[1] Most acute angle evaluated as 10, widest angle as 1.
[2] Ratios based on dry weight.
[3] Tuber production per hour of daylight per gram of dry leaf.

For the purposes of this bulletin "vegetative growth" refers to all plant parts except tubers and roots. The latter were not weighed in several series.

MORPHOLOGICAL RESPONSE OF PLANTS TO EXPERIMENTAL TREATMENTS

The principal characteristics of the plus-N plants are very briefly summarized on a comparative basis in Table 3. The basis for comparison was the appearance of the plants at the close of each series. This enables one (Figs. 2 to 6) to visualize the effect of day length and temperature upon plants receiving nitrogen continually. Additional details concerning the morphological response of these plants as exhibited at various periods of growth, as well as the response of plants from which nitrogen was withheld during various periods, are presented in the ensuing discussions and tables pertaining to the various plant parts.

TOTAL GROWTH AS MEASURED BY TOTAL WEIGHT OF THE PLANT

Most investigations on record, as cited by Liebscher (*68*) and by Wilfarth, Romer, and Wimmer (*136*), report that as plants became older the total dry weight of the entire plant continued to increase, but that if grown to approximately normal maturity the weight of the tops decreased during the last days or weeks when tuberization was still taking place, partly with the aid of materials translocated from the tops. Their experience and the results of this investigation show that during the very early periods growth was slow while still being made at the expense of the seed piece. When plants became photosynthetically more active because of new leaves, growth occurred and the vegetative portions (leaves and stems) increased rapidly in size, number, and weight until tubers formed. Then total weight increase continued at an active rate but consisted largely of tuber production and finally as this slowed down the weight increased very little. The extent, proportion, and duration of growth of the various plant parts and of the entire plant were greatly altered in these investigations by temperature, photoperiod, and nitrogen nutrition (Fig. 7, Tables 4 and 5).

In this investigation, with plants receiving nitrogen continually (1, 2, 3) the total dry weight of the entire plant increased throughout the duration of each series. The mean increment of gain for each day or each hour of daylight increased to a maximum and then decreased (Table 6, a and b). This maximum rate was attained during the third period in Series A and C. In Series D it was attained during the second period—heat damage during the third period having

FIG. 2.—Type of plant growth produced by the close of each period when nitrogen nutrition was altered in Series A, with days long and warm. Numbers at lower left designate the lots. Small numbers to right give dates photographed. Inside diameter of pots was ten inches in this and other figures.

caused the rate of gain to decline rather abruptly. Plants of Series B were still adding weight at an accelerated rate on the 79th day when the last set was harvested (Fig. 7).

Because of their greater total leaf surface, the greatest gains per day or per hour of sunshine were produced by longer-day plants (A and D). Later when tubers were forming the hourly growth rate was increasing with the inter-

TABLE 4.—*Mean fresh weight per plant, in grams, of various parts of plants harvested at the close of each period, after being grown under different conditions of nitrogen nutrition during days of different length at several temperatures.*

Period after which harvested	Series A 80° to 76° F. 14.5 to 12 hours				Series B 70° to 62° F. 10.8 to 9.2 hours				Series C 60° to 64° F. 10 to 13.3 hours				Series D 72° to 92° F. 14 to 15 hours				Series DS 72° to 92° F. 10.5 hours	
LEAVES [1 2]																		
First	38.4				10.2				14.8				27.1					
Second	97.0		57.9		43.5		27.8		86.7		52.7		117.7		76.2		109.2	51.1
	85.6		37.5															
Third	140.8	100.2	38.7	38.6	53.8	46.2	37.6	27.7	153.6	131.8	92.6	58.1	143.7	141.1	94.8	64.8		
	43.0	41.5	22.9	16.9														
Fourth	112.1	43.0	63.8	14.4	62.6	46.9	42.7	23.5	128.0	73.5	80.4	27.9	61.1	86.1	46.3	28.3		
	16.4	7.5	21.4	5.8														
ABOVE GROUND STEMS, PETIOLES, AND MIDRIBS [1 2]																		
First	37.3				8.8				7.3 4.6				35.1					
Second	148.5		81.9		27.1		18.2		46.3		24.5		175.6		107.1		100.4	53.9
	162.0		96.1						30.7		13.8							
Third	188.7	64.3	64.6	89.7	28.8	27.0	17.6	15.5	115.0	100.7	53.9	41.9	269.9	278.3	141.4	138.1		
	169.1	64.2	58.1	91.2														
Fourth	220.0	182.4	116.6	68.9	29.9	27.7	19.7	15.6	103.0	91.6	46.5	33.5	286.2	302.6	143.9	100.8		
	156.4	112.4	91.4	61.2														
UNDERGROUND STEMS AND STOLONS [3]																		
First	5.8				2.8				4.6 1.1				5.8 1.3					
Second	16.7		12.5		3.3 0.9		3.0 0.8		7.2 3.5		6.2 3.2		13.1 9.3		11.1 9.8		13.5 3.2	9.6 1.8
Third	27.1	24.9	16.2	12.5	3.8 1.0	3.1 1.1	2.7 0.8	3.6 0.8	7.1 4.1	7.2 4.2	7.0 3.2	5.2 3.0	14.5 12.6	16.5 18.5	12.8 11.3	12.7 10.9		
Fourth	18.6	24.9	16.2	14.6	3.4 0.6	3.4 0.6	3.2 0.7	2.4 0.7	6.8 4.0	6.2 4.0	5.8 4.8	5.9 3.3	17.1 17.6	19.3 21.0	14.3 17.8	10.9 10.2		

	TUBERS																	
First	0				1.05				0.04				0				63.8	32.6
Second	5.59		32.05		48.0		45.6		57.2		74.1		0.55		8.3			
Third	154.8	164.7	83.6	98.0	148.5	127.3	96.0	84.6	379.1	351.5	239.1	180.5	22.5	21.5	77.6	66.5		
Fourth	235.6	213.3	150.0	116.6	226.1	189.0	159.9	124.3	503.9	448.7	297.3	231.7	22.8 36.1	11.6 69.3	64.3 65.3	72.3 92.3		
	TOTAL OF VEGETATIVE PARTS																	
First	81.5				21.8				32.3				69.3				226.3	116.4
Second	509.		285.9		74.8		49.8		173.7		100.4		315.7		204.3			
Third	568.5	493.6	330.2	248.9	87.4	77.2	58.7	47.6	279.8	243.4	156.7	108.2	440.7	465.0	260.2	226.3		
Fourth	523.4	370.3	304.3	165.2	96.5	78.6	66.3	42.2	241.8	176.3	137.5	70.6	382.0	439.9	224.2	150.4		
	TOTAL OF ENTIRE PLANT EXCEPT ROOTS																	
First	81.5				22.8				32.4				69.3				289.1	149.0
Second	515.4		318.0		122.8		95.4		231.0		174.5		316.3		212.6			
Third	723.4	658.3	413.8	346.9	235.9	204.5	154.7	132.2	658.9	594.9	395.8	288.7	463.2	486.5	337.8	292.8		
Fourth	759.0	583.6	459.3	281.7	322.5	267.6	226.2	166.5	745.7	625.0	434.8	302.3	404.8	451.5	288.5	222.7		

[1] When two numbers appear in one table, space upper line is for leaves or stems from upper half, lower line from lower half, in A.
[2] In Series C, data on upper lines are from midribs and petioles of compound leaves, lower lines from above-ground stems only.
[3] Data on upper lines from underground stems, on lower lines from stolons.

TABLE 5.—*Mean dry weight in grams per plant, of various parts of plants harvested at the close of each period, after being grown under different conditions of nitrogen nutrition during days of different length at several temperatures.*

Period after which harvested	Series A 80° to 76° F. 14.5 to 12 hours				Series B 70° to 62° F. 10.8 to 9.2 hours				Series C 60° to 64° F. 10 to 13.3 hours				Series D 72° to 92° F. 14 to 15 hours				Series DS 72° to 92° F. 10.5 hours	
LEAVES [1 2]																		
First	4.10				0.88				1.42				2.81					
Second	12.30		7.67		3.95		2.35		9.00		4.96		14.89		9.81		12.28	5.97
	9.08		4.82															
Third	19.88	17.41	12.93	8.94	5.30	4.39	3.45	2.49	16.07	12.49	9.08	5.42	20.37	19.50	13.11	10.33		
	9.56	8.91	5.44	5.81														
Fourth	25.29	18.20	14.76	7.74	6.21	4.42	4.34	2.78	17.40	12.36	9.81	5.44	20.05	25.28	14.33	10.06		
	6.86	5.40	5.81	3.66														
ABOVE GROUND STEMS, PETIOLES, AND MIDRIBS [1 2]																		
First	2.12				0.32				0.27 0.20				1.52					
Second	10.14		5.78		1.17		0.77		1.98		1.04		13.43		8.97		5.79	3.48
	12.01		7.53						1.53		.71							
Third	11.29	10.95	6.72	5.89	1.41	1.30	0.82	0.68	5.52	4.78	2.47	1.99	19.63	21.22	10.87	11.13		
	12.76	11.43	6.69	6.37														
Fourth	15.41	14.05	8.60	6.53	1.60	1.58	1.05	0.82	5.65	5.01	2.39	2.05	23.20	25.13	10.67	11.18		
	11.23	9.57	6.91	5.54														
UNDERGROUND STEMS AND STOLONS [3]																		
First	0.48				0.18				0.27 0.07				0.39 0.08					
Second	2.12		1.74		0.28		0.27		0.58 0.32		0.49 0.39		1.29 0.82		1.37 1.14		1.17 .30	0.97 0.23
Third	2.64	3.74	1.85	1.48	0.30	0.26	0.22	0.24	0.64 0.32	0.62 0.30	0.54 0.24	0.43 0.23	1.76 1.12	1.94 1.68	1.48 1.10	1.49 1.06		
Fourth	2.09	2.68	1.91	1.63	0.29				0.60 0.34	0.60 0.30	0.46 0.23	0.46 0.22	1.82 1.52	2.82 1.80	1.55 1.56	1.24 1.01		

TUBERS																
First	0				0.13				0.01				0			
Second	0.64		4.10		6.19		6.10		7.60		11.06		0.07	1.09	7.79	4.05
Third	17.99	22.46	9.04	12.09	20.03	20.26	14.29	13.52	58.78	58.46	35.53	31.98	2.30	2.40	8.31	7.28
Fourth	29.84	26.67	17.27	14.16	38.28	34.43	26.94	21.04	88.29	83.64	50.09	42.57	1.88	1.08	5.93	8.08
Fifth													1.28	5.94	3.23	8.47	8.48	7.16
TOTAL OF VEGETATIVE PARTS																
First	6.70				1.38				2.22				4.80			
Second	45.65		27.54		5.40		3.39		13.40		7.60		30.43	21.29	17.54	10.65
Third	56.13	52.44	33.63	28.49	7.01	5.95	4.49	3.41	22.35	18.18	12.33	8.07	42.88	44.34	26.56	24.01
Fourth	60.88	49.90	37.99	25.10	8.10	6.26	5.62	3.80	23.99	18.27	12.89	8.17	46.59	55.03	28.06	23.52
Fifth													53.92	55.08	31.11	25.90	23.45	12.06
TOTAL OF ENTIRE PLANT EXCEPT ROOTS																
First	6.70				1.51				2.23				4.80			
Second	46.29		31.64		11.59		9.49		21.00		18.66		30.50	22.38	27.33	14.70
Third	74.13	74.90	42.67	40.58	27.04	26.21	18.78	16.93	81.33	76.64	47.86	40.05	45.18	46.74	34.87	31.29
Fourth	90.72	76.57	55.26	39.26	46.38	40.69	32.56	24.84	112.30	101.90	62.98	50.74	48.47	56.11	34.04	31.57
Fifth													55.20	61.02	34.34	34.40	33.81	19.22

[1] When two numbers appear in one space, upper line is for leaves or stems from upper half, lower line from lower half, in A.
[2] In Series C, data on upper lines are from midribs and petioles of compound leaves, lower lines from above-ground stems only.
[3] Data on upper lines from underground stems, on lower lines from stolons.

TABLE 6.—*Mean daily and hourly gain in total dry weight per plant and percentage of the total gain occurring in the vegetative portions during the various growth periods.*

Period	Series A 80° to 76° F. 14.5 to 12 hours				Series B 70° to 62° F. 10.8 to 9.2 hours				Series C 60° to 64° F. 10 to 13.3 hours				Series D 72° to 92° F. 14 to 15 hours			
(a) MEAN DAILY GAIN IN GRAMS OF TOTAL DRY WEIGHT PER PLANT																
First	0.304				0.095				0.124				0.319			
Second	1.389		0.875		0.469		0.371		0.918		0.802		1.714		1.173	
Third	1.513	1.495	0.596	0.483	0.793	0.750	0.476	0.382	3.230	2.962	1.537	1.125	1.545	1.710	1.315	0.938
Fourth	1.185	0.115	0.898	–.095	0.879	0.658	0.626	0.360	2.380	1.935	1.164	0.824	0.940	2.680	–.251	0.113
Fifth													0.763	0.534	0.039	0.314
(b) MEAN GAIN IN MILLIGRAMS OF DRY MATTER PER HOUR OF DAYLIGHT																
First	20.5				9.1				11.9				22.5			
Second	98.6		62.2		47.8		37.8		77.2		67.6		117.3		80.2	
Third	115.3	113.8	45.4	36.8	85.9	81.4	51.6	41.4	266.8	244.8	127.0	93.0	103.0	113.8	87.6	62.4
Fourth	95.4	92.7	72.4	–7.7	91.8	70.5	67.1	38.6	186.3	151.5	182.2	64.5	62.3	177.8	–16.7	39.6
Fifth													50.5	35.7	2.6	20.8
(c) GAIN IN VEGETATIVE PARTS[1] DURING VARIOUS PERIODS AS PER CENT OF INCREASE BY ENTIRE PLANT																
First	100.0				93.7				100.0				100.0			
Second	98.4		83.6		39.4		25.2		59.5		32.6		99.9		93.8	
Third	59.8	21.1	46.2	23.9	10.4	3.6	11.8	0.6	24.8	18.3	24.2	11.5	84.8	85.7	42.2	30.4
Fourth	28.6	0.0	34.4	0.0	5.7	2.1	8.2	4.9	4.6	0.2	4.4	1.1	100.+	100.+	100.+	54.7
Fifth													100.+	1.0	100.+	85.4

[1] Vegetative parts are considered as all of plant except tubers and roots.

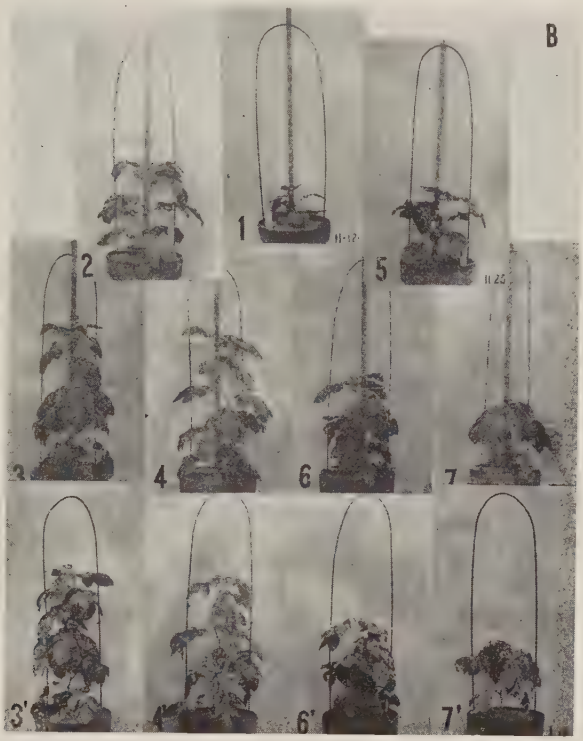


FIG. 3.—Type of plant growth produced by the close of each period, with different nitrogen nutrition, in Series B, with short days and low temperature. Arrangement of plants as in Figure 2. All pots ten inches in diameter.

mediate-day and short-day plants (C and B) but decreasing with the long-day plants. When consideration is given to differences in light intensity and a coefficient is secured by dividing the mean hourly gain in dry weight per plant by the mean hourly number of gram-calories of radiation, the gains in total plant weight during the second period of each series were very similar and during the third and fourth periods the cool-short-day plants had the greatest gains or could be considered most efficient in adding total weight.

The total green weight of tops increased with the length of day and the temperature. However, the total green and dry weights of the entire plant were highest with the low-temperature, intermediate-day-length plants (C) because of their very great tuber production. The short-day, low-temperature plants (B) were the smallest, having the lowest weight of

FIG. 4.—Type of plant growth produced in Series C, in which days were increasing from short to intermediate length and temperature was constantly low. Nitrogen treatments and arrangement of plants as in Series A in Figure 2. Pots ten inches in diameter.

tops and of total plants, on both the green and dry weight basis. Top and total weights of short-day, high-temperature plants (DS) were much lower than those of the comparable long-day plants (D).

Withholding nitrogen (5, 7, 4) always resulted in lower weight of the top and entire plant than when nitrogen was continued (except when leaves of continual-nitrogen plants were damaged by heat as in 3D), and adding nitrogen always resulted in higher values.

Supplying nitrogen to starved plants at the end of the second period always increased the total weight, and the daily and hourly increments continued to increase when the increments in weight were decreasing in plants of all other treatments, except in Series D where there was a rapid decrease in total weight during the period of excessive temperature. (For probable reason for unusual performance of Series D see pages 108 and 109).

FLOWER DEVELOPMENT

A relatively high rate of carbon assimilation or the accumulation of carbohydrates in the tops seems necessary for flower formation in the potato. Broili (*16*) was able to increase the number of seed balls, without adversely affecting tuber production, by girdling the stalks. Similar results have been obtained by gassing the plants with carbon dioxide (*14*). Garner and Allard (*41*), growing potatoes at high temperatures, found that blooming was increased by shortening the day from 18 to 14 hours and that with days of 10 and 5 hours flowers formed but did not open. Arthur, Guthrie, and Newell (*6*) did not secure blooming with ten-to-twelve-hour (normal winter) days but even though they obtained it with 18- and 24-hour days they greatly increased it by adding carbon dioxide to the air. The theory advanced by Knight (*60*) that non-fruiting is due to tuber development, as demonstrated by increased b ooming when tubers were removed during growth, is not borne out by more recent work. Arthur (*6*) secured some of the best tuber yields from p.ants that bloomed most profusely. East (*32*), repeating Knight's exper-

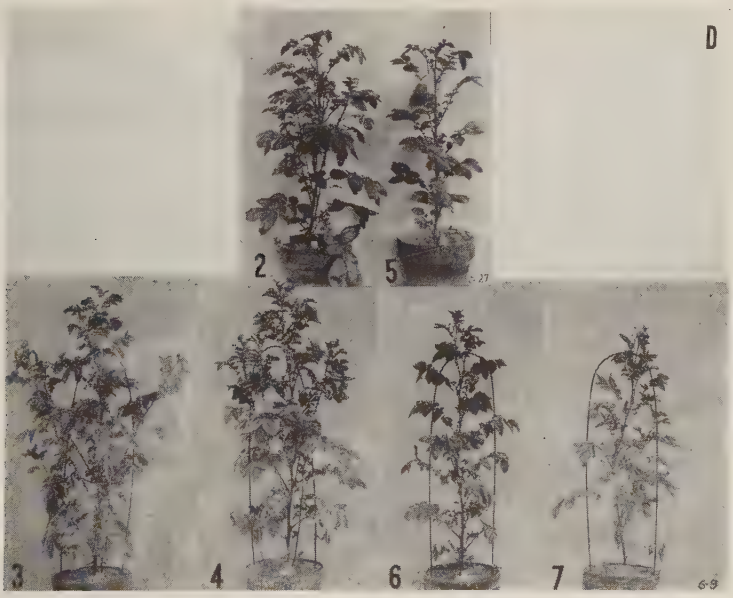


FIG. 5.—Type of plant growth produced in Series D, in which long, warm days were increasing both in length and temperature. Arrangement same as in Figure 2, except that the picture of the plant typical of those harvested at the end of the first period is omitted.

iments, found no relation between tuber removal and increased fruit setting. Young (*139*) reported a definite correlation between tuber and seed production and also a shedding of buds following a wave of warm weather in early summer. Stout and Clark (*114*) reported that plants of ten varieties (including Triumph) bloomed and tuberized profusely at Presque Isle, Maine, but that plants grown from the other halves of the same tubers at the New York Botanical Garden did not open a single flower before abscissing, although they did produce a good crop of tubers. Young (*140*) found that in the blasting and shedding of flowers under unfavorable weather conditions there is an early degeneration of both ovule and anther contents.

In these experiments with the plants grown at a high temperature and with long days of increasing length (D), large clusters of completely developed flowers terminated the main axis about 30 days after emergence (Fig. 5). Within the next ten days fully developed flowers in smaller cymes were produced on laterals growing from the axils of the third or fourth leaves from the top or from the laterals coming from the basal nodes. The nitrogen-deficient plants had the most flowers per cyme. With the high-temperature-and-decreasing-day-length series (A), the cymes were smaller and more of the flowers aborted as buds or abscissed prematurely than when the day length was increasing (Fig. 2). This was especially the case with the high-nitrogen plants. With both the series that were grown at low temperatures in short days, whether decreasing (B) or increasing (C) in length, the flowers never developed beyond barely distinguishable primordia (Figs. 3 and 4). Although variation in the nitrogen salt supply caused distinct differences in regard to vegetative growth and stolon and tuber development, it was a relatively less important factor in so far as flower development was concerned. There was a tendency for nitrogen curtailment to increase the number of blooms per inflorescence and to prolong the length of time they remained attached.

FIG. 6.—Typical plants of Series DS 27 days after emergence after being grown during a 10.5-hour day at high temperatures with nitrogen since emergence (2) or without nitrogen during the last 12 days (5).

That length of day rather than the inorganic nitrogen supply or temperature

was the factor dominating flower development was demonstrated by the plants growing at a high temperature and given only a 10.5-hour day (DS). On these plants flowers did not develop beyond the primordial stage characteristic of the low-temperature series. No seed balls were developed by any plants in any series.

There is no evidence that there was any relation between the extent of flower production and tuber production. Apparently elongation in the potato plant is genetically limited to a fairly definite number of nodes. When these have been differentiated the primordium of an inflorescence is initiated but whether it develops entirely, part way, or hardly at all

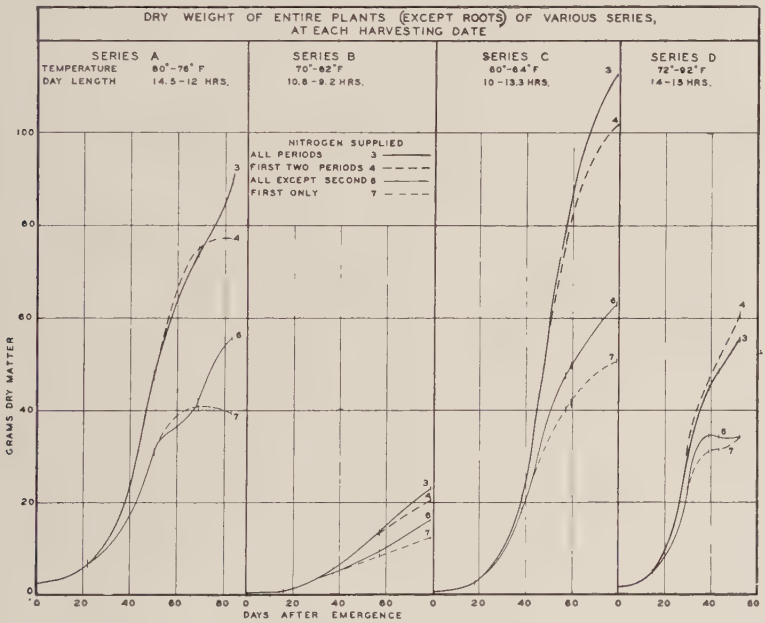


FIG. 7.—Total dry weight (except roots) produced per plant at different dates in each series with various nitrogen treatments.

is dependent upon the physiological conditions within the plants. This internal condition is a result of the external environment.

When carbohydrates are formed very rapidly, in quantities in excess of the needs of the enlarging cells of the stem tip or of the embryonic leaves, as in high-temperature, long-day plants, flowers may be formed before the greater part of the nitrogen flow is diverted to lateral buds, which elongate as the next step in vegetative growth. When days are short, blos-

som buds are not developed beyond primordia. Conditions appear unfavorable for nitrogen assimilation in these tops, as has been shown to be the case in tomatoes by Eckerson (*35*).

STEM DEVELOPMENT AND GROWTH

Internal characteristics.—The stems of the continual-nitrogen plants grown with long days and high temperature (A) soon became very thick (9-15 mm. at the base), woody, and stiff with extensive development of secondary xylem, being comparable in internal appearance to the long-day tomato stems of Pfeiffer (*96*). The stems of short-day and low-temperature plants were slender (4-6 mm. in diameter) with very little woody tissue and practically no rigidity, showing anatomical characteristics of the 5- and 7-hour tomato plants of Pfeiffer (*96*). The stems of the short-day, low-temperature plants (B) were thinner and had less woody tissue than those at high temperature (DS). Those of intermediate day length (C) had a slightly greater diameter and more secondary xylem than those of Series B.

The withholding of nitrogen from the nutrient solution, causing the development of a less vegetative stem, resulted in an increase in the proportion of xylem to the pith, as was found in tomatoes (*64*). As the nitrogen supply became exhausted the activity of the cambium was reduced until finally the differentiated secondary xylem and phloem cells were adjacent to each other. When nitrogen was added to starved plants, cambial activity in the stems was renewed and the new secondary xylem was visible as a distinct zone similar to the tomato stems shown by Kraus and Kraybill (*64*).

With the extremely high temperatures encountered during the very long days of the third and fourth periods of Series D, the new stem growth was relatively thinner and not so stiff as formerly. This condition was due to the reduction in the differentiation of woody tissue when respiration was excessive, thus simulating the condition in tomatoes grown at comparable temperatures (*92*). Jones, McKinney, and Fellows (*54*) found that stem diameter of potatoes increased with rising temperature to a maximum at 14°-15° C. and then decreased, so that stems of 30.5° C. plants had diameters only 40 per cent as great.

The central axis.—The central axis of the experimental plants generally had between 10 and 14 nodes, from which stolons developed below the surface of the sand and generally from 15 to 19 leaves with axillary buds and eventually lateral shoots above the surface, or a total of about 25 or 30

buds along the main axis. The deve'opment of these buds into lateral stems and stolons is discussed in separate portions of this paper.

Jones, McKinney, and Fellows (*54*) secured increased height of stem with increases in soil temperature from 11° to 27° C., and then much less growth at 27° to 30.5° C. than at any of the lower temperatures. They also found that the green weight of tops reached the maximum at 21°-21.5° C. and then decreased very rapidly. Bushnell (*18*) concluded that with soil and air temperatures the same there was no significant difference in stem elongation in a series grown at 20° to 29° C. when axillary shoots were kept pinched out. The etiolated conditions of all of these plants, as shown by his photographs, may have had a bearing on his results. Beaumont and Weaver (*11*) more than doubled the average stem length in seedlings by increasing the night temperature from 50° to 60° F. (day temperature about 5 degrees higher). They also increased the stem length as the length of day was increased from 9 to 18 hours. At 50° F. the increase was only 11 per cent, compared with 104 per cent at 60° F. All workers report similar gains in top growth with increased photoperiods (*6, 31, 41, 81, 99*). The effects of nitrogen in increasing stem growth was very well shown by the triangle nutrition experiments conducted by Johnston (*52*).

TABLE 7.—*Mean height above the surface of the sand of the central axis of the plants continually supplied with nitrogen in each series.*[1] *(Measured at close of fourth period.)*

Lot No.	Periods when nitrogen was supplied	Mean height per plant in centimeters				
		Series A	Series B	Series C	Series D	Series DS
3	All	44.2	29.8	48.5	86.2	59.0
4	1st, 2nd	38.6	55.2	43.3	84.1	.....
6	1st, 3rd, 4th	46.4	27.2	33.3	81.4	.....
7	1st	44.5	25.7	27.4	84.8	51.0

[1] Central axis measured to tip of inflorescence or rudimentary evidences of it.

In this investigation the length of the central axis increased as the amount of light increased: for example the plants growing in days increasing in length from 10 to 13 hours (C) had a longer central axis than those in days decreasing from 10.8 to 9 hours (B) (Figs. 10 and 9, Table 7). This occurred even though the temperature was higher during the early part of the period with Series B than with Series C. At high temperatures with a 10.5-hour day (DS) the main axis was much shorter than with days of 14 to

15 hours (D) but longer than with plants grown in days of comparable length at low temperatures (B, C) (Figs. 9 to 12).

The above-ground portion of the central axis was short when nitrogen was withheld from the nutrient solution early in the season—7 in Figures 8 to 12. It was altered but little if nitrogen was not withheld until late, *i.e.*, after tuber de-

FIG. 8.—(Left) Typical stem growth of plants from each of the nitrogen treatments of Series A, as the plants appeared at the close of the third period. All axes to scale from actual measurements.

FIG. 9.—(Upper right) Same for plants of Series B.

FIG. 10.—(Lower right) Same for plants of Series C.

velopment was well under way (4). Increasing the nitrogen supply late in the season (6) may have increased the length of the central axis, but only very little.

Lateral stems: development and growth.—Elongation of buds in the axils of the leaves began about the time the flower primordia developed at the terminus of the central axis (page 28). Axillary elongation occurred from both the basal and apical buds of the above-ground stem with practically no growth from the median buds. With plants in a highly vegetative condition stolons frequently came to the surface and produced normal stems with leaves as did the lateral stems coming from the above-ground buds.

Almost invariably the shoot coming from the axil of the third leaf below the terminal inflorescence developed into the dominant one. The shoot from the fourth axil generally grew and was only slightly shorter than the one from the third axil, and sometimes equal in length. The buds in the axils of the top and second leaf very rarely developed lat-

erals. This was probably due to the very meager development of these leaves, the upper one sometimes being barely discernible. As the lateral stems represented most of the stem growth in all except one series (B) the discussion given for total growth will suffice for laterals also. Complete data are given in Table 9.

When days were long and warm, the apical growing points of many stolons came to the surface and produced leaves and stems (Figs. 2, 5, 8, 11), but when days were short (Figs. 3, 4, 6, 9, 10, 12) this did not occur. This aspect is considered in the discussion dealing with stolons.

FIG. 11.—(Left) Typical stem growth for each of the nitrogen treatments of Series D as plants appeared on June 8 at the close of the third period.

FIG. 12.—Typical stem growth of plus (2DS) and minus (5DS) nitrogen plants of the 10.5-hour, high-temperature series (DS) as they appeared on May 30 at the close of the second period.

Growth of each of the major laterals was similar to that of the central axis. The characteristic number of leaves developed along the lateral axis, which then terminated in an inflorescence. Linear growth was then continued by the lateral or laterals which developed in the axils of the third or fourth leaves below the terminal. This process was repeated till eventually laterals of fourth rank removed from the central axis were being developed (Figs. 8 to 12). The length of each succeeding rank of laterals became shorter (Table 8). Lateral development of this kind occurred only with the high-temperature, long-day plants, the short-day low-temperature plants barely developing any primary or first-rank laterals.

Nitrogen withdrawal at the end of this first period reduced the number and length of all types of laterals, but most

TABLE 8.—*Effect of nitrogen supply under long, warm day conditions of Series A upon mean number and length per plant (in centimeters) of aerial laterals of various ranks and origins.*

Lot number	Date measured	Mean length of central axis	Laterals from stolons		Laterals of various ranks from aerial nodes								Total number and length of aerial stems	
					First		Second		Third		Fourth			
			No.	*Length*	*No.*	*Length*	*No.*	*Length*	*No.*	*Length*	*No.*	*Length*	*No.*	*Length*
2A	August 20	42.6	2.2	104	12.7	309	5.9	50	.....	.....	.....	.....	20.8	505.6
5A	August 26	44.4	1.5	82	12.0	219	1.6	8	.....	.....	.....	.....	15.1	353.4
3A	September 10	44.2	3.3	139	11.6	293	17.6	195	15.2	50.0	1.6	2.6	49.6	723.8
4A	September 10	38.6	2.0	86	9.1	279	14.9	201	8.1	30.8	0.3	0.4	34.4	635.8
6A	September 10	46.4	2.5	109	8.4	191	16.6	91	6.9	13.8	.....	.....	34.4	451.2
7A	September 10	44.5	2.0	87	11.6	230	8.1	61	0.6	1.5	.....	.....	22.4	424.0

especially those of second rank and beyond. Withholding nitrogen at the end of the second period almost completely checked the growth of laterals coming from stolons but much elongation still occurred in laterals of second, third, and fourth rank, thus suggesting a deficit of assimilated nitrogen in the lower portions of the plant, as contrasted with the upper parts, which used translocated nitrogen as well as the unassimilated soluble nitrogen in the leaves and stems of the upper portions of the plant. Late nitrogen addition (6) increased the number of second- and third-rank laterals more than any other type.

With plants growing at high temperatures during long days (Series D) the first laterals to develop when nitrogen was supplied constantly were from the axils of the lower leaves. In the early part of the season, during the first and second periods, longest laterals developed in the axils of the first fully developed leaves, *i.e.* the third and fourth from the base. Laterals at successively higher nodes were successively shorter (Fig. 13). During the next (third) period the inflorescences developed and linear growth of the central axis was terminated. The laterals in the apical axils then elongated very rapidly and while the total elongation of the basal laterals was almost as great, the rate of increase was less rapid. At all periods growth of laterals from axils in the median portion of the stem was very limited and practically did not increase as the season advanced.

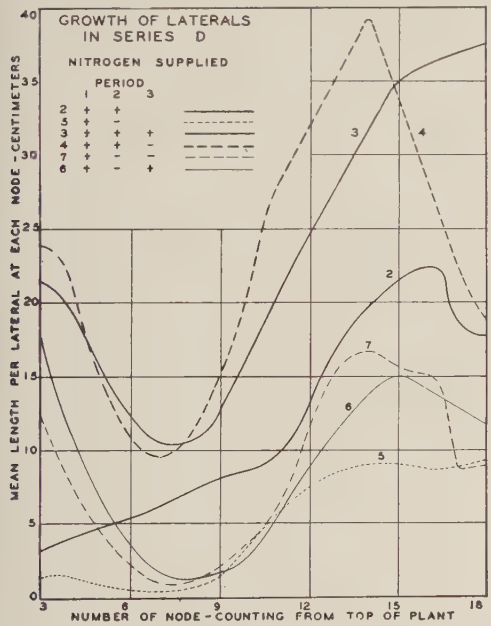


FIG. 13.—Extent of growth of lateral stems in the various leaf axes of plus and minus nitrogen plants of Series D at the close of the second and third periods.

When nitrogen was withheld from the plants during the second period after emergence (5D), the total growth of the lateral stems was cut to half that of continual-nitrogen plants. During the second period the growth of each of the lower six laterals was about equal. At higher levels they were very much shorter, with practically no elongation of the laterals by the end of the second period in the upper half of the plant. During the third period the laterals from the two lower nodes practically ceased growth, but those from the third to seventh basal nodes elongated. The apical laterals elongated very rapidly, approaching the length of the corresponding laterals of the high-nitrogen plants. The median laterals still did not grow.

When large vegetative plants were deprived of nitrogen after the second period (4D), the immediate effect was a check in the growth of the four lowest laterals and an increase in that of the fifth to tenth laterals, as compared with the high-nitrogen plants. The lower leaves of these plants were dying off rapidly as a result of the nitrogen shortage, whereas those of continual-nitrogen plants remained green; hence the difference in growth of the lower laterals. There was no significant difference in the elongation of the apical laterals. Greater elongation of laterals located at the fifth to tenth nodes was due to the green leaves located here probably having encountered less competition for nutrients than did correspondingly located leaves of high-nitrogen plants (3D).

The addition of nitrogen at the close of the second period increased the length of the laterals from the two basal and eight apical nodes but those from the median nodes were not as long as those of plants that were still starving. These laterals were comparable but not yet equal in growth to those of the continual-nitrogen plant.

Results with the other summer series (A) were somewhat similar. With nitrogen continually supplied, apical laterals accounted for the highest percentage of total elongation, followed by the laterals coming from stolons. When the nitrogen supply was limited (7A and 4A), the percentage of total linear growth in the basal laterals was higher. With a high nitrogen supply the aerial laterals from stolons accounted for a greater percentage of the total lateral growth and the basal laterals less than when nitrogen was not supplied. This was especially the case when nitrogen was added late in the season (6A) (Table 8).

Linear growth of stems.—The total linear growth of all aerial stems was most rapid during the period immediately

TABLE 9.—*Mean length per plant, in centimeters, of all lateral stems and of all aerial stems.*

Period after which harvested	Series A 80° to 76° F. 14.5 to 12 hours				Series B 70° to 62° F. 10.8 to 9.2 hours				Series C 60° to 64° F. 10 to 13.3 hours				Series D 72° to 92° F. 14to 15 hours				Series DS 72° to 92° F. 10.5 hours	
ALL AERIAL STEMS (LATERALS PLUS MAIN AXIS)																		
First	27.1				32.4				19				52					
Second	505		352		51.7		37.0		57		27		269		162		152	90
Third	724	656	451	424	61.0	54.5	38.8	39.7	97	74	41	37	495	534	241	231		
Fourth	Not measured				71.1	68.9	44.4	37.3	100	100	47	37	Not measured					
ALL LATERAL STEMS																		
First	1.0				0				0				9					
Second	463		308		10.9		2.3		13		1.6		191		84		93	29
Third	679	597	410	380	21.0	9.8	0.9	0.3	48	26	2.8	1.7	409	450	158	146		
Fourth	Not measured				29.4	19.6	8.5	0.4	41	30	2.6	1.7	Not measured					

following the development of the leaves on the main axis, but in all series considerable elongation was occurring in aerial stems throughout the life of all plants when nitrogen continued available. The greatest linear growth occurred in plants grown at high temperatures during long days (A, D) and least with short days and low temperatures (B, C). When day length was increasing, elongation continued for a relatively longer time and was more extensive than when it was decreasing (Table 9).

Withholding nitrogen resulted in a serious check in the growth of stems in all series but elongation did not cease completely until plants were almost dead, some elongation still occurring even after most of the leaves were dead. Elongation after nitrogen was withheld was least with short-day, low-temperature plants and greatest with long-day, high-temperature plants on both a relative and an absolute basis. The total length of the stems after nitrogen was withheld had increased at the termination of the various series as follows: Series B after 52 days, 16 per cent; Series C after 53 days, 96 per cent; Series D after 28 days, 345 per cent; Series A after 43 days, 472 per cent. These figures refer to Lot 7 as compared with Lot 1.

When nitrogen was not withheld until the end of the second period, elongation was again most extensive when days were warm and long. The percentage increases of length at the end of the fourth period over the length when nitrogen was withheld at the end of the second period (Lot 4′ compared with Lot 2) were as follows: Series B, 33 per cent; Series C, 75 per cent; Series D, 98 per cent.

This extensive elongation of N-deficient plants under high-temperature, long-day conditions was undoubtedly accomplished by the breaking down of organic nitrogen to soluble forms and the subsequent translocation of such soluble nitrogen as well as other compounds from the older parts of the plant (*92*). When the experiments were terminated this had generally continued to the point of all leaves being dead except a few at the tips of laterals.

Supplying nitrogen to plants from which N was withheld during the second period always increased the linear growth —but only to a slight degree beyond that which occurred in plants deprived of N still longer. The nitrogen going into the tops apparently was used to rehabilitate the leaves, by rebuilding the chlorophyll supply, and also to enlarge the leaves.

LEAVES

Bushnell (*18*) and also Beaumont and Weaver (*11*) reported greater division of the compound leaves as temperature was increased. Bushnell found leaves to comprise a lower percentage of the weight of tops at 29° C. than at 20° C. and the leaflets were also a paler green and more narrow. Beaumont and Weaver noticed a decreasing pubescence at 50° compared with 60° F. Shick (*109*) found that shortening the day length resulted in a visible broadening of leaves.

In the first two leaves that developed just above the surface, the apical leaflet was always large and round and frequently the lateral leaflets were not differentiated, there being only a pair of more or less developed lobes at the base of the leaf. These leaves seldom lived more than a few weeks. The third and higher leaves differentiated leaflets, the type and extent of differentiation and development varying with environmental conditions (Figs. 2 to 6).

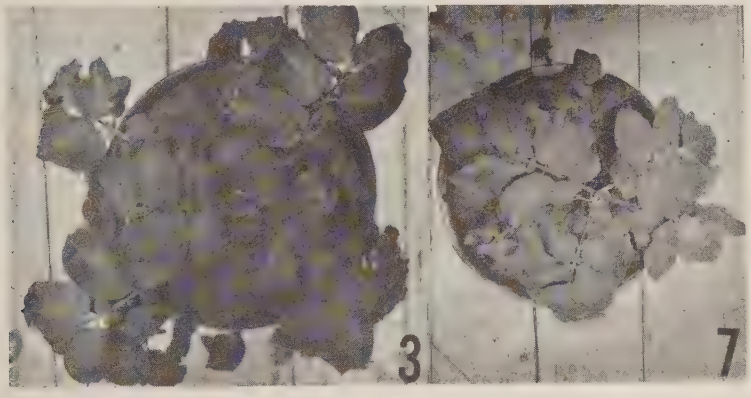


FIG. 14.—View from top of plants of 3B (left), 7B (right), showing cessation of leaf differentiation, especially apparent in 7B.

With a continual nitrogen supply with low temperature and days of intermediate length (C), each leaf was generally divided into three pairs of large, broad, overlapping lateral leaflets of almost equal size that generally were larger than the apical leaflet, and the folioles or leaflets of second and even third rank were well developed. The leaves were dark green and thin, drooping down from the midrib. The petiole of the compound leaf came out from the stem at a wide angle (45°) and the midrib curved downward because of the weight of the leaflets and lack of supporting tissue. The lower leaves remained green and did not die off much in advance of the

others. As the season advanced and days became longer, the upper leaves developed characteristics tending toward those produced on long-day plants.

Under the shorter-day conditions of Series B with temperature about the same, the leaves were about the same as in C or if differing the leaflets were a trifle paler green, larger, broader, and thinner, wilting more easily during bright days (Fig. 15).

With the less favorable long-day, high-temperature conditions of Series A and D, from four to six pairs of lateral leaflets were produced by compound leaves that were smaller. In these the apical leaflet was almost always definitely larger than the lateral ones. The apical pairs of lateral leaflets were decidedly the largest, the others tapering off rapidly to a fifth, sixth, or even seventh more or less rudimentary basal pair. The leaflets were relatively thick and flat but under the more extreme conditions they were folded up along the midrib. The compound leaf came out from the stems at a sharp angle (20°-25°) and the midrib was stiff and straight. When the days became longer and warmer (D) the upper leaves became smaller and stiffer, were folded more, and had more leaflets per leaf, and the lower leaves died off more rapidly. On the other hand when the days became shorter and cooler (as in A) the upper leaves showed many of the characteristics of Series B and C.

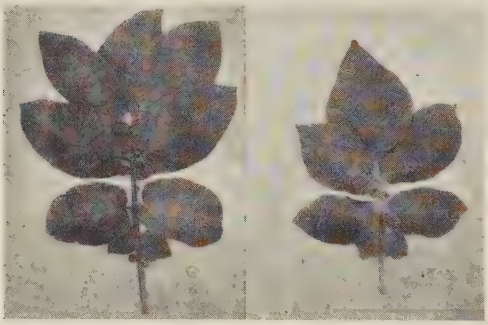


FIG. 15.—Leaves from plus-N (left) and minus-N plants (right) grown at low temperatures with short days (Series B).

When the temperature was intermediate to high and days were short (DS), the leaves were at an angle and almost as stiff as in the long days, but the size and development of the leaflets were more like those of short-day, low-temperature plants, including extensive growth of folioles, dark green color, and thin leaves.

Withholding nitrogen after the first period caused the leaflets to become chlorotic, first along the margins and then, as the entire leaflet became yellow, the leaf margins became pigmented. They became flat and rigid or else folded or

rolled up along the midrib. The leaflets that were not fully developed when nitrogen was withdrawn were smaller and longer than those of the continuous-nitrogen plants. The leaves came out from the stems at a sharper angle. The apical leaflet was relatively larger than the lateral ones and there was more rapid tapering off in size from the apical to the basal pair of laterals than in continuous-nitrogen plants.

In Series B actual counts made 18 days after nitrogen withdrawal from the solution revealed 7.5 per cent fewer pairs of leaflets, compound leaves 15 per cent shorter, and lateral leaflets averaging 8.5 per cent shorter and having a ratio of width to length of 0.58:1 compared with 0.64:1 in leaflets of continual-nitrogen plants. The lower leaves died off first, the upper ones, on the central axis and at the tips of laterals, remaining green until the last. These plants matured several weeks early because of the early death of their leaves.

With high temperatures and long days, nitrogen-deficiency symptoms appeared quickly and distinctly, but leaves continued to be differentiated for a considerable time after nitrogen had been withdrawn (Tables 4 and 5). With short days and low temperatures practically no new leaves were differentiated after nitrogen was withdrawn. Instead the uppermost leaves continued to grow until they were practically as large as the older lower leaves; thus at a very early date these plants had the appearance of plants that have completed their growth, a distinctive but later-occurring characteristic of the continuous-nitrogen plants of Series B (Fig. 14). The leaves of low-temperature, short-day plants turned to a pale, whitish green color in Series B or a chrome yellow color in Series C, and while apparently devoid of chlorophyll they remained alive in this condition for a long time. Even the lower leaves did not turn brown and die early.

Withholding nitrogen from older plants, *i.e.* at the end of the second period, always checked the leaf growth promptly and in all ways caused a response very similar to that produced by withholding nitrogen from younger plants. With short days and low temperatures (B, C) the leaves turned a pale green and then yellow but remained alive for a long time. With long-day, high-temperature plants (A, D) the lower leaves died off quite soon after nitrogen was withheld and the upper leaves remained green, and small new leaves continued to be formed. In the case of the plants grown as days were getting longer and hotter (D), the nitrogen reduction brought about changes within the leaves that increased their resistance to heat. When subjected to exces-

sive temperatures (120° F.) only about 35 per cent of the leaves were killed in contrast with 75 per cent when nitrogen was supplied continually. This enabled these plants to continue to function after this period of stress. Their weight of leaves and of tubers increased while in the continual-nitrogen series they decreased.

Addition of nitrogen to old plants after being starved during the second period brought back a dark green color into practically all the leaves and prolonged the life of the lower leaves as compared with plants continuing to be without nitrogen. Old leaves were enlarged but new leaves were not produced when temperatures were low and days very short (B), but when days were of intermediate length (C) a few new leaves were produced, while with high temperatures and medium (A) or long days (D) a number of new leaves were produced quickly and continuously until the experiments were terminated. In the latter case the soft leaves were severely damaged by heat during the third period.

LEAF AND STEM GROWTH COMPARED ON THE BASIS OF DRY WEIGHT

With nitrogen continually supplied the greatest total dry weight of leaves per plant was produced with long days and high temperature (A, D) (Tables 4 and 5). With regard to leaf weight in proportion to stem weight, the short-day and low-temperature plants produced the most leaves, *i.e.*, had the highest ratio of leaf to stem (Fig. 16). The significant effect of a short day in increasing leaf growth is shown in Series DS, where the leaf/stem ratios were greatly increased above comparable long-day plants of Series D. As plants became older, the leaf weight increased most in short days with low temperatures, while in long days and high temperatures the stem weight increased most. This effect is also seen in Series A, where the leaf/stem ratio increased as the temperature and day length decreased.

The total dry weight of leaves was approximately six times higher with long warm days (A) than with short cool days (B), yet the tuber production of the latter series was distinctly the greater of the two (Table 5).

When nitrogen was withheld at the end of the second or third period the total dry weight and ratios of dry weight of leaves to stems were greatly reduced, mostly with low temperatures and short days. Under the long-day, high-temperature conditions, nitrogen was utilized by the growing points of the tops to form stems and leaves, but with short days new leaves were not sent out and the tuber growth appeared to absorb most of the unassimilated nitrogen remaining in the plant.

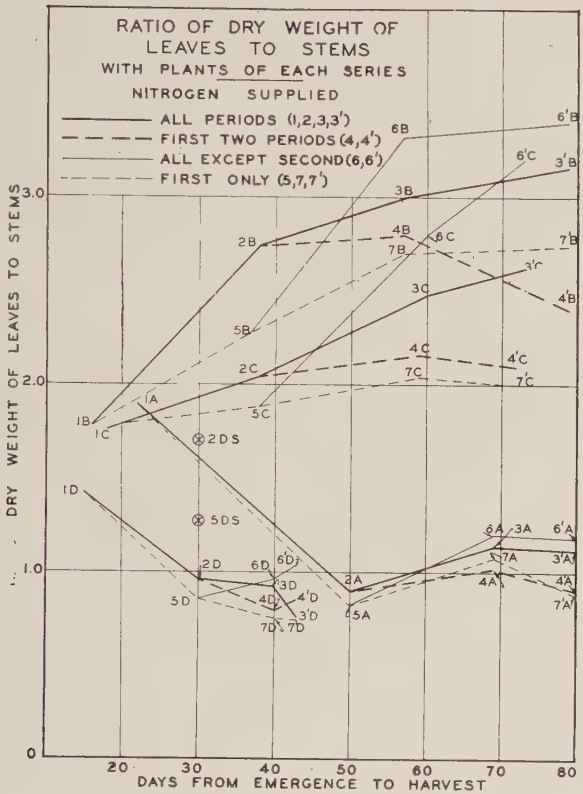


FIG. 16.—Ratio of dry weight in leaves to that in stems (including stolons) for various nitrogen treatments in each series.

With nitrogen supplied to N-deficient plants at the end of the third period, the increase in dry weight of leaves in all series was relatively more rapid and the ratios of dry weight of leaves to stems were much higher than with the constant-nitrogen plants. Most of the late-season increase in weight of the tops was in the leaves either as new leaves (A, D) or enlarged and revived leaves (B, C). The plants matured like high-nitrogen plants rather than like the nitrogen-deficient plants (Figs. 2 and 6).

TOP GROWTH AS MEASURED BY INCREASE IN WEIGHT

The green weight of the tops or vegetative portions (all of plant except tubers and roots) increased as the season advanced until a maximum was reached just prior to the

period of most active tuberization (Tables 4 and 5, Figs. 23 and 24). The dry weight of the tops continued to increase throughout the duration of these experiments.

The largest and heaviest tops were those produced in long warm days (A, D); the smallest and lightest were those produced in short days with low temperatures (B, C). An increase in day length of only 2 to 3 hours (C compared with B) trebled the dry weight of the tops at low temperatures. Increase in the day length of 3.5 to 4 hours at a high temperature (D compared with DS) only a little more than doubled the highest total dry weight of tops. The top weight of the short-day plants at a high temperature (DS) was approximately three times as great as the weight of those grown at low temperature (B) but some of the difference was also due to greater light intensity accompanying the higher temperature. Tops were increased both by increasing the length of day and increasing the temperature, within the ranges of this experiment. In another set of plants grown during the summer of 1933 at temperatures averaging 85° F. throughout the life of the plants (E), the weight of tops (data not reported) was less than in the Series A and D.

The weight of tops was a rapidly decreasing percentage of the total dry weight with each successive harvesting period, decreasing with greatest rapidity with short-day, low-temperature plants (Tables 6C and 18). When days were becoming longer and hotter (D) the relationship was reversed, the tops continuing to increase in weight while tubers decreased.

When nitrogen was withheld at the end of the first period the green weight continued to increase for a time and then decreased at an earlier date and more rapid rate than when nitrogen was supplied constantly. The dry weight followed similar trends but more slowly, not having started to decrease when the last plants were harvested in any of the short-day series (Lot 7′, in B, C, and DS), and having decreased only temporarily in the long-day, high-temperature series (7DS). The percentage of dry matter going into the tops decreased still more rapidly with time than with the continual-nitrogen plants. Here too as days were getting hotter and longer (7′ DS), top growth came to constitute an increasing percentage of the total increase in dry weight.

When nitrogen was withheld from older plants (4) at the end of the second period, trends were similar to those with plants starved earlier, except that the percentage of weight going into the tops was very much smaller and decreasing more rapidly with time than in any other treatment.

Adding nitrogen to the nutrient solution after the plants had been starved during the second period (6) caused an abrupt and greatly accelerated increase in top growth. When conditions were least favorable for vegetative growth as in short days (B, C), the dry weight percentage going into tops was very greatly reduced after the initial rise. When days were long and warm the tops continued to represent a large percentage of the total weight, even increasing while tuber weight was decreasing (D). These plants died off more quickly than did those that continued to be deprived of nitrogen during the later periods (Table 6C).

The persistence of top growth even when sometimes accompanied by decrease in weight of tubers as found in plants receiving nitrogen during long warm days, together with the rather sudden death of the leaves and their reduced heat resistance, may have been due to conditions similar to those discovered in the tomato by Nightingale (*92*). He found that at 95° F. nitrate was assimilated very rapidly, but that there were no carbohydrate reserves because of their utilization in protein synthesis and respiration. As this condition persisted the carbohydrate supply became inadequate for protein synthesis. Then complex proteins were broken into simple amino compounds. After a short period of accelerated growth the plants died. As the potato plant has a lower optimum than the tomato, the temperatures with which plants of Series D were growing (period means of 85°-92° F.) were excessive in a similar degree. The plants not only used up the carbohydrates in the tops but also those stored in the tubers.

STOLONS

Hardenburg (*47*) found that at 68° F. the Rural New Yorker variety grown in a greenhouse at Ithaca, N. Y., during the late winter and spring produced more stolons, more branch stolons, and more green weight of stolons than at 59° F. Clark (*21*) found no correlation between tuber weight and stolon length but his data indicated a tendency for upper stolons to produce smaller tubers.

Wenkel (*132*), using short- and long-stolon varieties, found that stolons cease elongation as soon as the tip begins to swell into a tuber but that the various stolons on one stem do not stop elongating at the same time. He found that length increased with increased soil moisture and fertility and that length was increased more by manuring on heavy than on light soils, apparently because manured soils were more open and physically less resistant to stolons. He reports, from his work and that of others also, that it is char-

acteristic of some varieties, especially after late summer rains, for plants shortly before ripening to send out several more stolons which are longer and thicker than the others, but that tubers borne on such stolons are formed too late to attain marketable size. In the long-stolon variety Preusen, the number of stolons increased during a period of four weeks but with the short-stolon Erdgold the number increased during only one week. He states that the first termination of stolon elongation occurs with certainty when blossoms fall.

Shortening the days decreased the length of stolons of the South American varieties used by Shick (*109*). When all days were short (10 hours) Razumov (*99*) secured only 19 per cent as much stolon weight as when all were long (15-19 hours). He also found that short days early in the life of the plant greatly reduced the weight of stolons but that when they occurred late they caused but little difference. Very long days were so favorable for stolon formation that when tuber-producing plants were exposed to long days the stolons renewed growth and developed vegetative shoots above the soil surface. With a very long day (18-19 hours) at high temperature Garner and Allard (*41*) also found stolons producing vegetative aerial shoots.

General morphological observations on stolons.—At each node of the underground stem of the potato plants there was developed a compound eye-like bud which when first differentiated had only one bud. Later generally two (though sometimes more) additional buds were differentiated in a lateral position. These buds at the nodes thus resembled the eyes of tubers more than they did the axillary buds of the above-ground stems. The first or central bud manifested its apically dominant position and was the first to elongate into a stolon. The elongation of the others was dependent upon subsequent circumstances (Figs. 17 to 22).

The first buds to elongate into stolons were generally those centrally located at what appeared to be the third to the fifth nodes from the base of the subterranean stem. The buds from adjacent nodes both higher and lower on the stem developed stolons a short time later, but the first stolons from the central nodes continued to be the longest until tubers were developed on their tips. At the base of the stem, between the old seed piece and what appeared by casual inspection to be the lowest bud or at least the one developing the lowest stolon, one could find by careful inspection (especially with the use of a hand lens) from two to seven buds. These were developed in all stages from those very close to the old seed piece, which were barely discernible as

differentiated bud groups, to the upper ones in which the central bud was elongated as much as one millimeter.

With low temperatures (60°-72° F.) the first buds elongated into stolons at about the time the sprouts were emerging above the surface (B, C). With higher temperatures (70°-85° F.) stolons were not initiated till the first few leaves were forming above ground (A). With very high temperatures (above 85° F.) and with long days (14-15 hours) stolons developed very late and were very small (E) but stolon formation occurred quite early at high temperature if the days were short (ES).

The various types of stolons will be distinguished from each other by the following terms:

Primary stolons are considered as those developing first and singly from each node. These primary stolons elongated rather rapidly immediately after being differentiated from axillary buds. From 9 to 12 primary stolons were generally produced per plant. Those in the lowest and highest positions were commonly not only produced later but were also generally the shortest and least likely to produce tubers.

Lateral stolons are stolons developing at the same node as a primary stolon but from lateral buds. They were developed later, under some conditions at the rate of one to as high as 6 or 7 laterals per node.

Branch stolons are those produced still later from the lateral buds on the primary stolons. No branch stolons were observed on any lateral stolons.

Under conditions very favorable for stolon growth, primary stolons frequently came to the surface and developed an aerial stem with leaves which functioned as did the main stem. Stolons were then produced from the numerous axillary buds of such top-forming stolons.

Tubers were generally and most frequently developed from the terminal buds of primary stolons; however, they were also formed from buds in any position on any type of stolon. Tubers were also produced as lateral bud enlargements directly on the main stem and on primary stolons without an intervening stolon.

Under some conditions the differentiation of new stolon axes and their elongation continued throughout the life of the plant. The most active period of stolon elongation preceded the period of most active growth of the aerial laterals, or about the time blossoms formed or should have formed. Generally with the initiation of tuber expansion, stolon growth throughout the plant was either entirely inhibited or proceeded at a greatly reduced rate. The development of the

TABLE 10.—*Mean number per plant of stolons of various types at the close of each period.*

Period after which harvested	Series A 80° to 76° F. 14.5 to 12 hours				Series B 70° to 62° F. 10.8 to 9.2 hours				Series C 60° to 64° F. 10 to 13.3 hours				Series D[1] 72° to 92° F. 14 to 15 hours			
PRIMARY STOLONS																
First	6.9				7.8				8.9				8.3			
Second	11.8		9.8		9.2		9.6		10.9		10.7		9.5		7.8	
Third	17.0	17.6	9.8	10.0	Not counted				11.2	9.8	10.0	10.0	6.3	9.3	7.3	10.3
Fourth	Not counted				9.0	9.1	8.2	7.7	10.2	8.7	10.3	10.0	Not counted			
LATERAL STOLONS																
First	Counted in with the primary stolons				1.4				3.1				2.4			
Second					2.0		1.6		11.1		7.1		9.3		7.3	
Third					Not counted				12.8	9.3	6.7	9.3	8.3	6.8	10.8	5.3
Fourth					1.3	3.7	1.8	3.0	9.1	9.3	7.0	8.5	Not counted			
BRANCH STOLONS																
First	0				1.6				0.7				0			
Second	11.5		4.8		1.8		3.5		4.3		3.9		3.5		9.6	
Third	17.5	13.4	3.5	2.4	Not counted				4.3	5.0	3.0	3.0	8.3	19.4	11.5	11.5
Fourth	Not counted				1.0	3.2	1.3	3.5	4.2	5.3	2.7	4.0	Not counted			
TOTAL NUMBER OF STOLON AXES PER PLANT																
First	6.9				10.7				12.7				10.8			
Second	23.3		14.7		13.0		14.7		26.3		21.7		22.4		24.7	
Third	34.5	31.0	13.3	12.4	Not counted				28.3	24.1	19.7	22.3	22.8	35.4	29.5	27.0
Fourth	Not counted				11.3	16.0	11.3	14.2	23.5	24.3	20.0	22.5	Not counted			
PRIMARY STOLONS COMING ABOVE SURFACE OF SAND																
Third	4.4	2.8	2.3	2.3	None to surface				None to surface				1.9	1.8	1.9	1.8

[1] Total number in 2DS was 26, in 5DS 18. Stolons in DS too short and close for classification but none came to surface

stolons as to place, extent, predominant type, etc., was very considerably altered by the various experimental factors introduced.

When conditions became so favorable for tuberization that no stolon growth was occurring, as in Series C, the upper two or three primary stolons appeared to be quiescent for a brief period and then died back from the tip. Sometimes almost the entire stolon rotted. At other times, as the tip was dying back, branch stolons near the base or lateral stolons at the same node renewed their growth and in a few instances small tubers developed at these places. This condition did not seem to be altered by nitrogen nutrition, being about alike with all treatments. At the same time the lower stolons also frequently failed to develop their tubers and shriveled but never were found rotting. The development of long, new stolons near the surface late in the season, as reported from German workers (*109*), did not occur in any series.

Growth of stolons when nitrogen was supplied continuously.—Although growing conditions had relatively slight influence upon the number of primary stolons, they apeared to have been most numerous when plants were grown at a low temperature with days of intermediate length (C, Table 10). At high temperature and with long days the terminals of a considerable number of stolons came to the surface and produced leaves. These stolons were commonly either the first stolons that elongated (the third to fifth from the bottom) or they came from the upper nodes located within an inch of the surface (Figs. 2, 5, 20, 21, 22). Under very hot weather conditions all the stolons commonly grew at a sharp angle toward the surface (Fig. 22). This did not occur with either low temperature or short days (Figs. 9, 10, 12, 18, 19, 21).

Increasing the day was the most efficient means of increasing the mean length of the primary stolons (Table 11). In Series C while day length was increasing from 10 to 12.5 hours the mean length of primary stolons was approximately twice as great as in Series B, where it was decreasing from 10.8 to 9.2 hours. Although the stolons were not measured, photographs of short-day, high-temperature plants (DS and ES) show the stolons to have been very short in comparison with the long-day plants (Figs. 21 and 22). The short days hastened tuber formation on primary stolon terminals; hence stolon growth was terminated early. When days decreased from long to intermediate length (A) the primary stolons were shorter than when the length was increasing (D).

TABLE 11.—*Mean length per plant, in centimeters, of stolons of various types at the close of each period.*

Period after which harvested	Series A 80° to 76° F. 14.5 to 12 hours				Series B 70° to 62° F. 10.8 to 9.2 hours				Series C 60° to 64° F. 10 to 13.3 hours				Series D[1] 72° to 92° F. 14 to 15 hours			
PRIMARY STOLONS																
First	12.6				21.4				3.0				30.2			
Second	70.3		51.1		31.6		27.2		65.6		67.3		75.6		69.1	
Third	100.5	117.9	55.4	51.6	Not measured				73.4	74.3	69.7	61.6	45.6	102.8	68.5	88.3
Fourth	Not measured				25.3	24.2	25.7	23.2	71.2	75.6	63.9	68.3	Not measured			
LATERAL STOLONS																
First					2.0				4.9				1.9			
Second	Measured in with primary stolons				2.1		3.0		15.0		7.3		38.2		28.1	
Third					Not measured				19.9	17.4	6.5	14.2	41.1	79.4	43.2	19.8
Fourth					2.0	5.7	2.8	5.4	13.9	13.8	11.9	15.4	Not measured			
BRANCH STOLONS																
First	0				1.0				0.3				0			
Second	31.7		8.0		1.2		2.3		3.3		2.3		9.0		24.3	
Third	32.4	20.1	6.8	5.6	Not measured				4.7	6.2	1.9	2.6	21.9	67.1	37.6	32.8
Fourth	Not measured				0.4	1.6	3.0	3.4	5.0	5.6	2.3	3.9	Not measured			
ALL STOLON AXES																
First	12.6				24.3				35.2				32.1			
Second	102.0		59.1		34.9		32.4		83.8		76.9		122.8		121.5	
Third	132.9	137.9	62.1	57.2	Not measured				98.0	97.9	78.1	78.4	100.3	249.4	149.2	140.8
Fourth	Not measured				27.7	31.4	31.5	31.0	90.0	94.9	78.1	87.6	Not measured			

[1] Mean total length per plant of all stolon axes of 2DS was 18.6 cm. and of 5DS 14.4.

The total length per plant of primary stolons increased in all series until tuberization was well under way, thus showing that some stolons made considerable growth after the growth of others had been terminated by the formation of a terminal tuber (Table 11). In three series the total length was less at the end of the third or fourth period than earlier. This was due to the rotting of upper stolons, which was probably instigated by their mobile contents being translocated to growing tubers on other stolons as in Series B and C, or to the top for maintaining life during a period of stress as in Series D.

Lateral stolons were numerous at low temperatures when the day length was increasing from 10 to 13 hours (C) and even more so at high temperatures with long days (D) (Table 10). With short days of constant length (DS and ES) or of decreasing length (B) the number of lateral stolons was very small, tubers having been set on the primary stolons at a very early date.

The mean length per plant of lateral stolons and also the total length were increased as days became longer (Table 11). Results with Series DS and ES indicate that increased temperature did not result in lateral stolon growth if days were short (Figs. 21 and 22).

Branch stolons were most numerous with long-day, high-temperature plants, largely because under those conditions many primary stolons came to the surface and produced leaves (Fig. 20). Thus these stolons could act more or less as independent units.

With low temperatures and short-to-intermediate days (C) the number of branch stolons, on the primary stolons that remained in the sand, was greater than with similar stolons on high-temperature plants (A, D). With Series C the total number of branch stolons per plant was less than in A or D because none of the primary stolons produced leafy tops. With short days, regardless of temperature, very few branch stolons were produced, but frequently, especially at high temperatures, tubers were produced directly from lateral stolon buds without any intervening branch stolon (Fig. 21).

Branch stolons as a group were relatively short, but nevertheless the mean length increased as the day length increased. With short days the branch stolons were extremely short, mostly because of the extensive development of tubers from lateral buds without stolons.

Of the total length of all stolons, the highest percentage occurred in the primary stolons. This percentage decreased

as the plants became older in all except the very-short-stolon, short-day plants, where little late growth occurred. In all series the lateral stolons contained a higher percentage of the total stolon length than did the branch stolons. Increasing the day length greatly increased the percentage found in the lateral stolons but did not greatly increase the percentage that consisted of branch stolons until the primary stolons got to the surface and produced functioning leaves as in A and D; then the branch stolons might have been considered as of lateral type.

Stolon growth with nitrogen supply altered only as stolons were developing.—The withdrawal of nitrogen at the end of the first period exerted little effect upon the number or length of all or of any types of stolons, when days had been short enough to induce early tuberization, during this period (B, C, DS, ES). When day length and temperature had not been favorable for early tuberization until about the time nitrogen was withheld (A), the number and length of all types of stolons were distinctly less than in those plants where nitrogen was continued. When temperature and day length were becoming increasingly less favorable for tuberization (D) the early withdrawal of nitrogen caused a distinct increase in the number and length of primary and branch stolons. The greatest response was in the branch stolons. The number and length of lateral stolons was not so great as when nitrogen was continued.

Withholding nitrogen at the end of the second period exerted no significant influence upon stolon growth except in Series D, where it increased the number and length of primary and especially of branch stolons, but only the length (not number) of lateral stolons (Fig. 20). There was a tendency of this same kind with the primary stolons of Series A and C.

Supplying nitrogen to plants after they had been starved during the second period, although it rejuvenated leaves, had little effect on the number of all types of stolons except for a definite increase in lateral stolons in Series D. The differences in length in all stolon types were so small and variable as to be of doubtful significance except in Series D, where the length of lateral stolons increased and that of primary stolons decreased (contents probably resorbed by top when under stress).

Stolon growth when changes in nitrogen supply began at planting time.—The results with Series A raised the question as to whether stolon development might not be influenced by nitrogen modifications made when the seed pieces were

planted or when plants were emerging, more than when modifications were made after most of the primary stolons were developing. To this end two supplementary tests were conducted.

TABLE 12.—*Effect of omission or addition of the external nitrogen supply during various periods after emergence upon plant growth in Series X. Data for each lot appear on each date line, in space corresponding to that in which lot number and nitrogen treatments appear in (a).*

Date harvested	(a) Designation and N history of various treatments (+ indicates when N was supplied and O when not supplied)							
Dec. 16	e1 0				a1 +			
Dec. 23	f2 00	e2 0+			b2 ++	a2 +0		
Jan. 7	g3 000	f3 00+	e3 0++		c3 +++	b3 ++0	a3 +00	
Jan. 24	h4 0000	g4 000+	f4 00++	e4 0+++	d4 ++++	c4 +++0	b4 ++00	a4 +000
	(b) Mean number of primary stolons per plant							
Dec. 16	4.5				5.0			
Dec. 23	5.4	5.8			5.1	6.0		
Jan. 7	6.9	7.5	8.6		10.0	8.1	8.2	
Jan. 24	5.7	7.4	10.8	11.1	11.4	9.9	7.9	7.0
	(c) Total number of stolon axes per plant							
Dec. 16	4.5				5.0			
Dec. 23	5.4	5.8			5.1	6.0		
Jan. 7	7.5	8.5	11.2		16.2	11.4	10.5	
Jan. 24	6.0	9.8	15.1	15.0	17.5	16.6	13.0	9.9
	(d) Mean number of stolon primordia on main stem							
Dec. 16	4.3				3.5			
Dec. 23	2.7	3.2			2.7	2.1		
Jan. 7	2.9	2.7	2.4		2.1	2.1	1.3	
Jan. 24	8.6	4.6	3.4	3.0	1.6	2.9	3.1	2.5
Feb. 13 *	....	....	3.4	4.6	3.7	2.5	3.1	3.6
	(e) Mean total length of stolons per plant (centimeters)							
Dec. 16	1.4				1.8			
Dec. 23	4.2	3.8			3.9	4.0		
Jan. 7	20.4	17.2	28.8		37.5	26.4	29.7	
Jan. 24	17.5	24.8	41.7	36.5	37.3	45.8	27.6	23.2
	(f) Mean height of main stems (centimeters)							
Dec. 16	10.0				10.4			
Dec. 23	11.5	13.2			13.7	12.3		
Jan. 7	15.8	30.4	34.6		37.2	28.8	20.3	
Jan. 24	19.8	36.0	54.9	49.6	57.1	45.8	32.9	28.4
	.....	.....	53.1	68.3	61.8	47.1	32.6	23.4
	(g) Mean total number of tuberous enlargements per plant							
Dec. 23	0.4	0.0			0.0	0.0		
Jan. 7	3.2	1.2	1.2		1.1	0.9	1.1	
Jan. 24	3.0	4.3	9.3	11.0	10.9	9.9	6.6	5.5
Feb. 13 *	....	....	11.6	5.6	8.5	9.2	9.0	4.2
	(h) Mean total dry weight of tops per plant, in grams							
Jan. 24	1.234	2.331	4.240	4.142	4.010	3.339	2.034	1.948
Feb. 13 *	.....	.....	5.150	4.625	5.765	4.025	2.382	2.070
	(i) Mean total dry weight of tubers per plant, in grams							
Jan. 24	1.347	0.606	0.634	2.694	1.349	2.932	2.547	2.001
Feb. 13 *	.....	.....	8.237	9.637	10.713	9.581	7.862	6.080
	(j) Percentage of total dry weight in tubers							
Jan. 24	52.2	20.7	13.0	39.4	33.7	46.8	55.8	50.5
Feb. 13 *	.....	.....	61.5	67.6	65.0	70.4	76.7	74.6

* From Jan. 24 to Feb. 13 all plants were grown without nitrogen.

In one supplemental series, seed potatoes planted in sand to sprout at 70° F. and watered with a nutrient solution containing nitrogen seemed to initiate stolons slightly earlier than when nitrogen was lacking. At a temperature of 58° F. there was little difference. The difference may have been due entirely to the earlier emergence and hence earlier development of the plants in the nitrogen series.

In another supplemental series designated as X, sprouting seed pieces started in sterile sand on November 21 were planted in sand in six-inch pots on December 7 and from then on nitrogen was supplied to or withheld from the nutrient solution as explained in Table 12. The temperature and light were as in Series B. Some of the larger plants, as the No. 4 sets of Xc, Xd, and Xe, were crowded toward the end of the experiment so as to cause more etiolation of stems or reduced daily growth.

FIG. 17.—Stolon and tuber growth at low temperatures during short days when plants received nitrogen for short periods early in their life or later (Series X). (For explanation of experimental treatments, see Table 12a.)

When the only nitrogen available for growth was limited to that stored in the seed pieces the number of primary stolons was almost as great nine days after emergence (Xe 1) as when nitrogen was supplied in the nutrient solution during this period (Xa 1). However, as the plants became older and the nitrogen supply in the seed pieces became exhausted, there was only a slight increase in number of primary stolons. With nitrogen supplied the number of stolons increased continually so that on January 24 there were more

than double the number on the nitrogen-starved series (Table 12, Fig. 17).

When nitrogen was withdrawn from the solution supplied to the younger plants the number of stolons continued to increase for a brief period and then remained stationary, but when withheld from the older plants (Xc 4) the numbers remained stationary.

When nitrogen was supplied to plants that had been starved since planting (Xe to Xh), the number of primary stolons was always increased and continued to increase till the experiment was terminated, the final number being proportional to the length of time nitrogen had been supplied.

Branch and lateral stolons, which appeared about three weeks after emergence, increased in proportion to the nitrogen supply. They responded to the addition of nitrogen more than did the primary stolons.

The number of buds differentiated at the base of the stem and developed in stages ranging from apparently dormant and barely distinguishable buds to those elongating but less than 1 mm. long and considered as primordial stolons, was lowest where nitrogen was available early in the life of the plant and highest where it had been withheld during the early periods. When nitrogen was withheld for a long time (Xh 4) or when it had been available only a brief time (Xg 4) these primordia were more advanced than where it had been continuously available.. Thus it might have been possible for relatively old plants to develop new primary stolons from the base of the main stem somewhat as described by Tussing (*122*).

The total stolon growth, as measured by total length, followed the general trend of the number of stolons. Late addition of nitrogen resulted in a very rapid growth of stolons. There is also some indication that while late nitrogen withdrawal curtailed top growth it may have caused a brief period of increased stolon elongation (Xc 3 and 4).

These results show that the number and length of stolons can be greatly altered by variations in the amount of nitrogen available during the early life of the plant but that changes made late, especially after tubers have set, are of much less consequence.

Effect of experimental conditions upon weight and dry-matter of stolons.—Growing conditions caused considerable difference in the thickness and composition of stolons. The diameter or thickness of the stolons was least at low temperatures and increased as the temperature was increased. The mean dry weight per centimeter of stolon length and per-

centage of dry weight were considerably greater with Series D than with C (Table 13). Stolons of Series B with short days and low temperature were not weighed separately but their very low weight per centimeter was self-evident, as they were only one or two millimeters in diameter. The percentage of dry weight and weight per centimeter was higher with medium-high temperatures and short days than with any other treatment (DS).

TABLE 13.—*Percentage of dry matter in stolons and mean dry weight per centimeter of total stolon length in nitrogen treatments of Series C, D, and DS. (For basic data giving mean dry weight of stolons see Table 5).*

Period when harvested	Series C 60° to 64° F. 10 to 13.3 hours				Series D 72° to 92° F. 12 to 15 hours				Series DS 72° to 92° F. 10.5 hours	
	Dry matter (*per cent*)									
First	6.52				6.15					
Second	9.14		12.16		8.92		11.60		12.6	12.5
Third	7.95	7.58	7.45	7.90	8.90	9.06	9.88	9.77		
Fourth	8.51	7.39	7.94	6.99	Not weighed					
	Mean dry weight (*milligrams*) per cm. of total stolon length									
First	2.05				2.43					
Second	3.85		5.11		6.61		9.39		16.1	16.0
Third	3.23	3.02	3.06	2.99	9.32	6.74	7.36	7.57		
Fourth	3.81	3.11	5.81	2.47	Not weighed					

With nitrogen supplied continuously the percentage of dry weight and the dry weight per centimeter of stolon length increased as the plants became older. When nitrogen was withheld at the end of the first period there was a very rapid increase in the stolon thickness and also in the weight per centimeter and in percentage of dry matter, during the next or second period. This was because of limited N assimilation which with concomitant decrease in top growth caused carbohydrate accumulation in stolons. This was followed in the third period by much lower percentages with a smaller decrease during the fourth period. These decreases were due to decreased photosynthesis plus increased respiration in the N-deficient tops and consequent reduced carbohydrate accumulation of stolons. (See pages 115-121.)

Addition of nitrogen to starved plants brought about a brief decrease and then an increase in percentage of dry matter due to a brief period of translocation of reserve carbohydrates for building tops and then accumulation with increased photosynthate from new and renewed leaves. The greater dry weight per centimeter of stolon length in C was due to translocation of a greatly increased amount of reserves through

stolons that were no longer growing (Fig. 19), while in Series D the weight per unit of length decreased because of the development of some new stolons and translocation to the tops, whose heat resistance was reduced by nitrogen addition.

The characteristics of Series D were distinctive. The stolons were of uniform thickness throughout most of their length till about the 15th to the 20th day. Then there was very little indication of tuberization at the stolon tip but instead each stolon attained a diameter just behind the apex about two or three times that at the base, the diameter becoming gradualy less from the apical to the basal portions. In the continual-nitrogen series a number of the older stolons came to the surface and produced aerial stems and leaves but where nitrogen was being withheld this general swelling of the stolons continued until about the 25th day, when tubers were differentiated. However, throughout the continuation of this series, when plants were not receiving nitrogen the stolons exhibited this tendency toward tapering thickness, receding from the apical end. This thickening very largely disappeared when nitrogen was again supplied (6D). With short days, stolons were uniformly thick, tubers being distinctly differentiated without any unusual amount of stolon tapering (Fig. 20).

TUBERS

The essential physiological facts concerning tuberization have very recently been stated concisely by Tincker and Darbishire (*119*) as follows: Storage in tubers is the sum of carbohydrates manufactured *minus* carbohydrates for growth requirements *minus* other local carbohydrate requirements (as storage more or less permanently in stems and dormant buds) *plus* residual carbohydrates in the seed piece.

In order to determine some of the fundamental causes of tuber formation it is esential to keep in mind the morphological nature of the potato tuber as a modified stem with its axis greatly shortened and its lateral members only weakly developed as "eyes" (*9*). When the stolon tip accumulates carbohydrates and develops a tuber a great deal of cell division is occurring and of course considerable elaborated nitrogen is required. This initial stage is relatively short and does not involve much increase in size. As carbohydrates continue to be supplied the parenchyma cells expand as much as 64 times their previous volume (*9*). Most of the expansion occurs in the parenchyma cells located between the xylem and inner phloem, in the pith, and a minor amount in the pericycle. As these cells store sugar and starch and the protoplasmic content of the cells is relatively meager, it is

evident that not much nitrogen is required for their later or final development. Cambial activity makes a relatively insignificant contribution to the increase in size of the tuber.

It must be recognized that a bud, either dormant or partly developed, must be available for expansion in order to make a tuber (*124, 125*). The buds most frequently utilized for tuber formation are terminal buds of stolons, but tubers are frequently developed from lateral buds on stolons or directly from buds on either the underground or aerial portions of the stem or directly from the eye of a mature tuber either with or without an intermediate stolon, and under some exceptional conditions small tubers are produced on or within the parent tuber. At other times sprouts or stems swell so extensively as to be quite tuberous in appearance (*124, 125*).

Review of literature on tuberization.—The importance of the presence of a bud for expansion into a tuber was shown by Vochting (*124*). When cuttings were planted so that only internodal stem tissue was below the surface, tubers were produced aerially, the underground portion having been incapable of producing adventitious buds. By darkening the apex of a primary shoot the growing point was converted into a tuber.

The studies on the development of "sprout" tubers, also referred to as "secondary", "premature tubers", "blind", "kindel" or "onderzeeers" (Dutch for submarines), are of value in determining some of the fundamental facts concerning tuberization. These tubers are formed directly from the old tubers and are separated from them only by stolons varying in length from several centimeters to a millimeter or less, or they are formed inside of the old tuber. Such tubers are formed while the potatoes are still in storage or after they have been planted. Halsted (*46*) reported observations and conclusions concerning the occurrence of such tubers in fields of potatoes in New Jersey and narrates that among English gardeners it is a regular practice to produce new tubers for winter market by keeping tubers of the previous year's crop in a cool place during the summer, rubbing off the sprouts as they appear, then in the fall planting them in sand at 60° F., and in three months harvesting a crop of tubers of considerable size, developed without leaves.

Premature ripening of tubers by drouth or heat at the close of the vegetative period was considered a predisposing cause of sprout tuber formation by Wellensiek (*131*) and Schilberszky (*104*). Freshly harvested Garnet Chili potatoes from Bermuda produced secondary tubers when planted but when treated with thiourea, ethylene chlorhydrin, or sodium

thiocyanate to break the rest period, normal sprouts were produced (*28*). On the other hand, sprout tubers of this kind have been produced by chemical treatment. Denny (*26*) calls attention to the "fatness of the buds" activated by treating Triumph potatoes with potassium thiocyanate. The author, in January-February, 1926, obtained prompt and rapid sprout growth from Triumph potatoes just emerging from the dormant period without any treatment. When such seed pieces were treated with a one per cent solution of sodium thiocyanate, growth was not appreciably altered but there was considerable tuberous thickening at the base of several stems. Seed pieces treated with a two per cent solution produced tubers on very short stolons and then in some cases sent up plants from these new tubers. With a four per cent solution about half of the seed pieces produced small tubers directly but these did not sprout. Doring (*30*) obtained sprout tubers by the introduction of quinol into seed pieces. He found that this effect was more pronounced early in the storage period and with late varieties, which at any particular time were supposedly less dormant than early ones. This is in line with the findings of Weiss and Brierly (*130*) that Green Mountain tubers produced more sprout tubers than did Irish Cobblers. Goss (*45*) also observed with spindle-tuber Triumphs that sprout tubers were produced if the tubers were planted before the normal completion of the dormant period.

Storage of seed potatoes at high temperature (50°-60° F.) was reported by Wellensiek (*131*) to have induced formation of many sprout tubers, whereas Schilberszky (*104*) found them when the potatoes had been chilled during storage and then were planted at temperatures too low for normal sprout formation. Most workers (*131, 130, 45*) agree that the condition was most serious when potatoes were planted in cold soils (37° and 48° F.), especially when dry. Storage in light retarded sprout tuber development but not greatly if storage was prolonged (*131, 76*). Wellensiek (*131*) reported the water content of the parent tubers and first sprouts to have been between 75 and 90 per cent. He suggested that each successive crop of sprouts taking up a higher percentage of the remaining water gradually lowered the water content of the tuber and thus increased the relative concentration of dissolved materials until the concentration in the sprout was high enough to form a tuber instead of a sprout. In this connection he reported that a 3 per cent potassium nitrate solution plasmolyzed the hairs on the first sprouts but that a 4.5 per cent solution was needed to plasmolyze those on the

fourth set of sprouts. Tubers with sections of the skin removed, which were dried over calcium chloride until they lost 40 to 50 per cent of their weight, developed sprout tubers at once when planted.

Appleman (*4*) reports that when tubers lost their capacity to produce sprouts they had lost only 8 per cent of the total solids, but though not reported the loss of water must have been much greater. Botjes (*15*) showed that potatoes planted in damp sand absorbed water through new roots so that as the sprouts grew the nutrients moved into the sprouts and the percentage of water increased in the mother tuber. Premature tubers were produced after repeated sprout removal even though the mother tuber was sucked full of water. He concluded that these sprout tubers formed because of the deficiency of nitrogen compounds created by the repeated sprout removal while there was still an abundance of carbohydrates, the young tubers being developed when there was insufficient nitrogen for sprout growth. Wellensiek (*131*) also thought that small tubers which were quickly exhausted by sprouting were more likely to produce sprout tubers. Magocsy-Dietz (*76*) concluded that any condition which checks elongation of the sprout causes little tubers to be formed at the base of the lowest nodes and then if the sprout is removed adventitious buds of endogenous origin are built closely around the tuber eyes and these produce sprouts in damp air but little tubers in dry air. These are nourished by growing inwards into the tuber.

The removal of several crops of sprouts regardless of later planting temperature caused sprout tuber formation, and the greater the number of crops of sprouts removed the earlier the sprout tubers developed (*131*). Appleman (*4*) found that as successive crops of sprouts were removed from McCormick potatoes, the tubers first lost their apical dominance, and that after the removal of eight or nine sprouts they lost the power of producing sprouts and instead produced a number of small tubers. He adds significantly that these tubers were produced "in a manner very similar to those frequently seen in severe cases of the spindling-sprout disease" and on another page he states that the spindling sprout disease appeared to be a response to unusually hot and possibly dry midsummer conditions when tubers were forming.

When one now considers tubers that are sprouting and are then handled in various ways, the work of Vochting (*125*) is useful in approaching an understanding of the fundamental processes underlying tuberization. He found that when sprouting tubers of the French variety Marjolin (called "Six

Weeks" in Germany) in darkness with abundant air and soil moisture at 25° to 27° C., roots and foliage shoots developed quickly but no tubers were secured, while at 5° to 7° C. no foliage shoots formed but tubers were produced at the ends of old sprouts, on new stolons, and on the mother tuber; that is, the growing points were tuberized. When transferred from the high to the low temperature the foliage shoots took on a horizontal direction and the formation of tubers began. Decreased respiration did not account for the tuberization at low temperature because it was not retarded by low pressure of oxygen. Germination in sand free from moisture gave no foliage shoots but only short roots and stolons with numerous tubers, regardless of temperature. When the initial high moisture supply was reduced when foliage shoots were 10-12 cm. long, elongation stopped and numerous small aerial tubers were formed. When the soil was moist but the air was dry, shoots soon assumed a horizontal direction and numerous basal branches appeared. In diffuse light and with moist soil, if the air was moist large leaves with long internodes were produced, but if the air was dry leaves were mere scales and internodes were short and thick, and basal stolons were produced. When tubers were placed upright between plates without soil, elongation of the apical shoot decreased as the light was increased and roots were inhibited. According to these results by Vochting, tuberization or processes approaching tuberization were brought about by conditions which checked the elongation of sprouts or which prevented the production of non-storage vegetative organs and thus created a surplus of carbohydrates. His results showed that under high humidity hydrolytic processes occurred and vegetative growth resulted whereas with low humidity storage organs developed as a result of condensation of simpler sugars to complex sugars and starch. This is in line with the recent work of Nightingale and Mitchell (*92a*), who found much greater carbohydrate accumulation in the tomato with low than with high humidity.

From the work of these investigators it appears that this tuberization which occurs by the mere translocation of material from the old tuber to the sprout tuber is associated with desiccation of tuber tissue and with nitrogen deficiency, while carbohydrates continue in abundance.

Dealing with normal plants growing under irrigation, Clark (*21*) concluded that in the Rural New Yorker variety all tubers were differentiated from stolon tips or "set" at about the same time and that final differences in weight of individual tubers were due to unequal growth rates rather

than to age. Later work by Smith (*111*) and observations by Tussing (*122*) have shown that tubers are frequently "set" during a considerable greater period of time. Within any variety or strain the time, duration, and extent of tuber setting can be altered considerably by environmental and nutritional factors.

Temperature has long been recognized as a factor influencing tuber formation and development. Results of various workers are in general agreement that the most favorable temperature for tuber setting and for securing maximum yields is between 15° and 18° C. (59°-64.5° F.) as determined in controlled experiments or by study of long-time yield and weather records (*94, 40, 110, 54, 47, 18, 19, 11*). Straw mulching, which reduces the temperature but also reduces soil nitrate content, almost invariably has increased tuber production during periods of high temperature (*36, 37, 133, 135, 20*). There is also unanimity in results showing that in warmer regions potatoes should be planted early so as to produce some of the tubers in early summer before temperatures become very high (*37, 98, 133, 20, 135*). Bushnell (*18*) showed that tuberization did not occur at high temperatures, 26°-29° C., with late-spring normal day length, because the increased respiration reduced the amount of carbohydrates available for storage in tubers, but that tuber production increased with lower temperature as the amount of respired carbohydrates decreased. He also secured evidence of more rapid translocation of carbohydrates with the lower temperature.

Garner and Allard (*41*) were the first to call attention to the photoperiodic sensitivity of the potato. With the McCormick potato growing with high temperatures at Washington they obtained no tubers with an 18-hour day. As the day was shortened to 14 to 15 hours there was abundant flowering but only light tuber production, while with a 10-hour day tuber production was at the maximum but there were no flowers. With a 5-hour day there was a sharp decline in tuber yield due to greatly reduced leaf area. Potato species and varieties from South America have been found to have a specific dependence upon a day of 12 hours or less when grown in the very long days in Russia (*31, 99*) and Germany (*109*). It was found that long days retarded but did not prevent tuberization in most European and American varieties. Varieties secured from Chili responded more nearly like European varieties than did those from northern South America (*30*). This, it was thought, was due to the longer summer days in Chili, somewhat more comparable to

those in Europe. Razumov (*99*) found that plants given long days (19-15 hours) early in life and short days (10 hours) later, produced a much greater weight of tubers than when days were continually long or continually short. But when the short days occurred early with long days later, the tuber yields were greater than with either long or short days continually, but they were lower than when long days were followed by short ones. In the long days large tops were developed which supplied abundant leaf surface for carbohydrate manufacture and then when vegetative growth was terminated by the short days, extensive reserves were available. With *Solanum demissum, S. acaule, Ullucus tuberosus,* and *Oxalis tuberosa,* tubers did not develop during long days that followed short ones but instead tubers which had formed during short days were frequently resorbed and grew out as stolons or tops.

All investigators have found that the largest tops are secured with the longest days and the most tubers with intermediate to short days, but when days are much shorter than 10 or 12 hours the reduced leaf area causes reduced efficiency to the point where tuber yields are reduced not only per plant but also in proportion to the leaf area.

The photoperiodic response could be changed somewhat by altering the temperature or the carbon-dioxide content of the air. Arthur, Guthrie, and Newell (*6*) found that with the normal winter day the tuber yield of Irish Cobblers was "poor" at 78° F. but "fair" at 68° F. When the day length of the 68° F. house was increased by six hours of electric light the tuber production was still only "fair", but when carbon dioxide was added the tuber yield was "very good", as was the case with 24 hours of artificial light plus carbon dioxide. However, at 78° F., when the day length was increased six hours, and to 24 hours of artificial illumination, with additional carbon dioxide the yield of tubers was poorer than with the normal winter length of day, although the top growth was greatly increased. When maximum tuber yields were secured with a 15-hour day, Beaumont and Weaver (*11*) found that increasing the day length to 18 hours reduced the yield 8 per cent at 60° but only 1.3 per cent at 50° F. (night temperatures).

Adams (*2*) found that photoperiodic response differed with varieties. McClelland (*81*) also found variety differences, the Lookout Mountain being most responsive to reduced day length and the Triumph least, with the Irish Cobbler responding to an intermediate degree. In Wales, where temperatures are relatively favorable for potatoes, Tincker (*118*)

got a small increase in tuber yield with one variety and a decrease with the other when the day was shortened to 12 hours, and a reduction in both varieties with days of 9 or 6 hours.

McClelland (*81*) found that the yield of tubers increased as the plants were further away from the area which received artificial illumination, which was used to increase the photoperiod from the tropical day length to one of 15 hours. Here again a variation in the intensity of this supplemental light affected the Lookout Mountain variety the most, and then the Irish Cobbler, while the Triumph was least affected.

Darrow (*24*) calls attention to the possibility that the response of plants to a period of illumination with electric lights may not be the same as to normal daylight since in Alaska, close to the Arctic Circle where daylight is almost continuous, some vegetables respond differently from the way they are reported to have done in controlled greenhouse experiments. For example, Pfeiffer (*96*) reported that a day of 17 or more hours (partly artificial light) was injurious to tomatoes but in Alaska excellent crops are produced with summer days of 20 hours. Arthur (*7*) also reported maximum dry matter production with tomatoes and tobacco when light intensity was reduced. In all of these instances when artificial light was used the source of the light was tungsten lamps which yield a high proportion of long (warm) and few short waves.

The effects of variations in soil, culture, temperature, moisture, photoperiod, or light intensity are to a considerable degree the result of the effect that they exert not only upon photosynthesis but upon nitrogen assimilation. Innumerable papers dealing with fertilizer experiments, etc., give abundant data on gross yields of tubers but almost none of them deal with the fundamental aspects of the relation of nitrogen to tuber initiation and growth or metabolism. Nitrogen has frequently been found to be the most important element in commercial fertilizers, especially in the regions where potatoes are grown in a relatively cool climate (*17, 127, 141, 82*). Berkner and Schlimm (*11a*) report greatly increased vegetative growth but reduced tuber production when large amounts of calcium nitrate were applied in field trials at Breslau. It has been reported that a shortening of the main tuber axis occurred when nitrogen and phosphorus were deficient in field plats and a lengthening when they were abundand but potash was deficient (*79*).

Undoubtedly much of the increased yield, improved type, and increased size of tubers secured with a straw mulch when potatoes were grown with high temperatures has been due to the demonstrated decrease in nitrate content of the soil, which thus limited vegetative growth and facilitated accumulation of surplus carbohydrates.

A number of papers by French and English workers give consideration to the theory that tuberization is dependent upon the presence of endotrophic mycorrhiza (*12, 13, 77, 83, 93*). This theory does not seem tenable in view of Laurent's (*67*) earlier results in obtaining tubercles from starch-free shoots grown in the dark with a 10 to 20 per cent sucrose solution or those of Molliard (*83*) in getting onion bulbs and radish roots to develop in sterile glucose solutions. Bernard (*13*) later modified his theory and considered tuberization as a state of hypertrophy brought about by increased osmotic pressure. Lutman (*74*), however, found osmotic concentration always low in tubers and highest in the aerial stems during the period of tuber formation. In view of these facts and the great body of literature showing tuberization to be the result of a nutritive balance, the mycorrhiza theory hardly justifies further consideration so far as the potato is concerned.

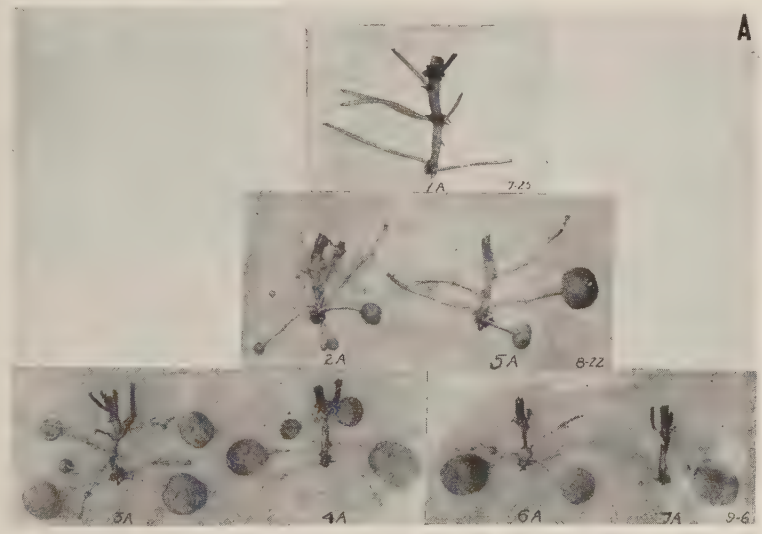


FIG. 18.—Stolon and tuber development of typical plants of Series A at the close of each of the first three periods.

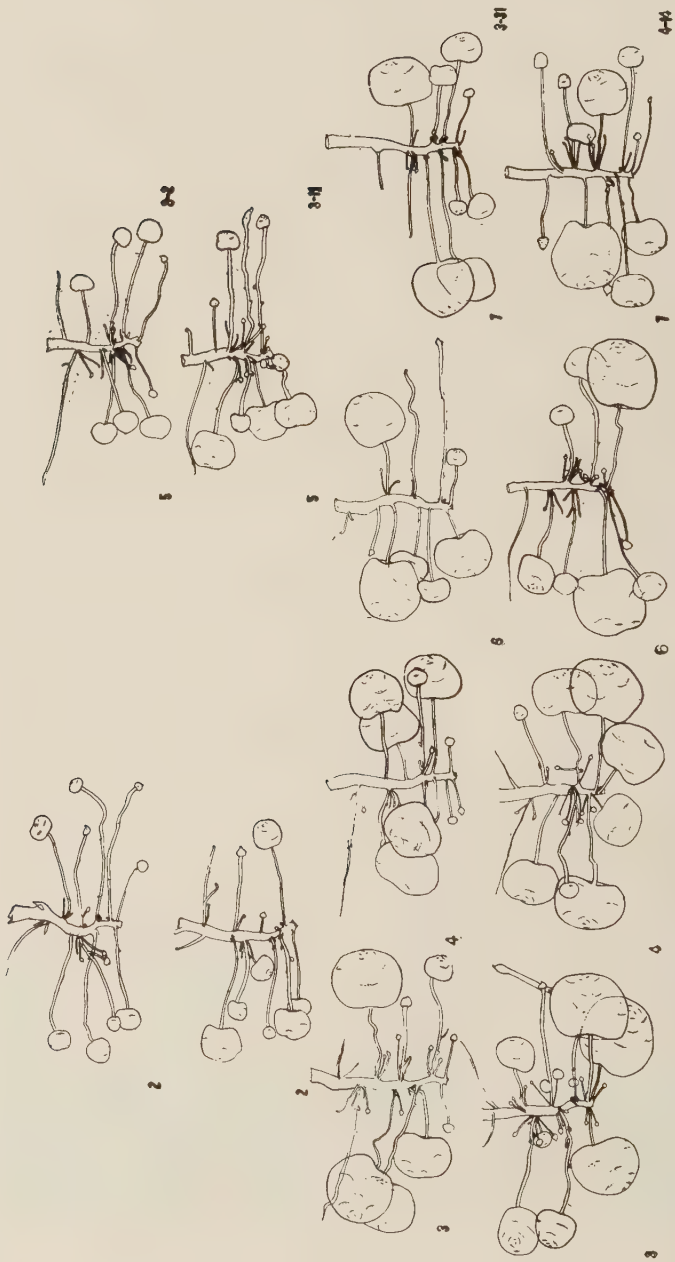


FIG. 19.—Sketches (made to scale) of stolon and tuber production by various dates with short to intermediate lengths of day at low temperatures (Series C). Actual length of underground portion of the main stem varied from 10 to 12 cm. for the various plants. Plant tops are shown in Figure 4.

Initiation of tuberization.—With a continuous nitrogen supply earliest tuberization occurred when days were short even though the temperature was relatively high (Tables 4, 5, 14, and Figs. 17 to 22). When short days were becoming shorter (10.8 to 9.25 hours) and temperature was low, tuber formation was rapidly under way 15 days after

FIG. 20.—Stolons and tubers produced by plants illustrated in Figure 5—grown at the high temperatures during long days of Series D. Upper row harvested 27 days after emergence, lower row 13 days later.

emergence (B) (Tables 4 and 5, Figs. 23 and 24). When the low-temperature days were becoming longer (10 to 13.25 hours) tuberization did not occur quite as early (C) (Fig. 19). When days were short (10.5 hours) but temperature was medium (72°-74° F.), tuberization must have occurred very early as shown by the high yields of tubers harvested the thirtieth day (DS) (Fig. 21). When days were long and temperature high, tuberization occurred earlier with the plants growing at 72°-74° F. (D) (Fig. 20) than in those at 86°-80° F. (A) (Fig. 18), even though the days were increasing in length from 14 to 15 hours with Series D while decreasing from 15 to 13.5 with Series A. In series E, which was grown at about the same time of the year as A but at a still higher temperature, tuberization had not yet begun at the end of 55 days (Fig. 22).

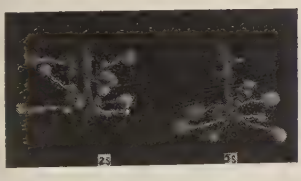


FIG. 21.—Stolon and tuber production from the short-day, high-temperature plants of series shown in Figure 6—harvested 27 days after emergence.

When nitrogen was withheld at the end of the first period from plants growing with long days (A, D) or with short to intermediate days (C), tuberization was initiated prompt-

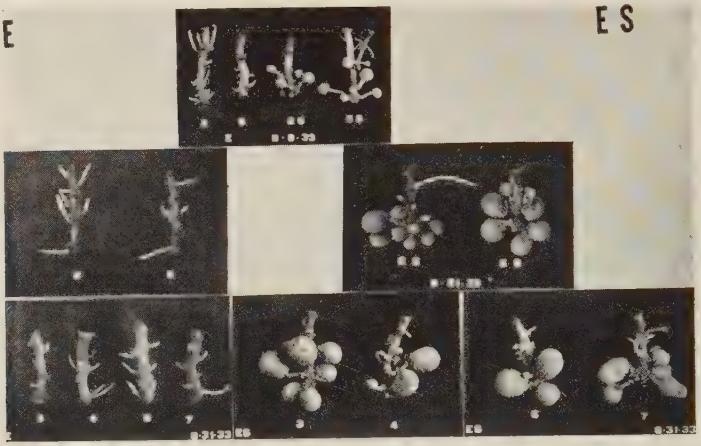


FIG. 22.—Tuber production in Series E and ES by different dates. Insertion of S in photographs to right indicates short day of 10.5 hours. Numbers under plants indicate standard nitrogen treatments. Dates of harvesting in lower portion of pictures.

ly or was greatly accelerated. With plants growing with short days that were getting shorter (B) or were uniformly short regardless of temperature (DS, ES), nitrogen withdrawal did not accelerate tuberization but retarded it, probably because of reduced leaf area. In the supplemental series (X) tuberization occurred earlier when nitrogen was withheld early (Table 12).

When the physiological balance of the plants tended to favor vegetative growth, a number of vigorous lateral buds were developed on stolons. When the balance shifted more toward one favoring tuberization, such as by elimination of nitrogen, lowering the temperature, or shortening the day, a number of these buds swelled into tuber primordia, but frequently, before they enlarged into small definite tubers, some other tuber or primordium on the stolon exerted dominance and these primordia developed no further or shriveled.

Rate and amount of tuber production.—When nitrogen was continually supplied the highest yield and greatest daily production of tubers came from plants grown at about the same low temperature (B, C, 60°-64° F.) but during days which were increasing in length from 10 to 13.25 hours (C) (Table 14), the larger leaf area of the short-to-intermediate-day plants (C) was responsible for their great yield

TABLE 14.—*Increase in dry weight of tubers calculated on the basis of daily gains per plant for each period and also mean increases per day and per hour of daylight per gram of dry weight of leaves.*

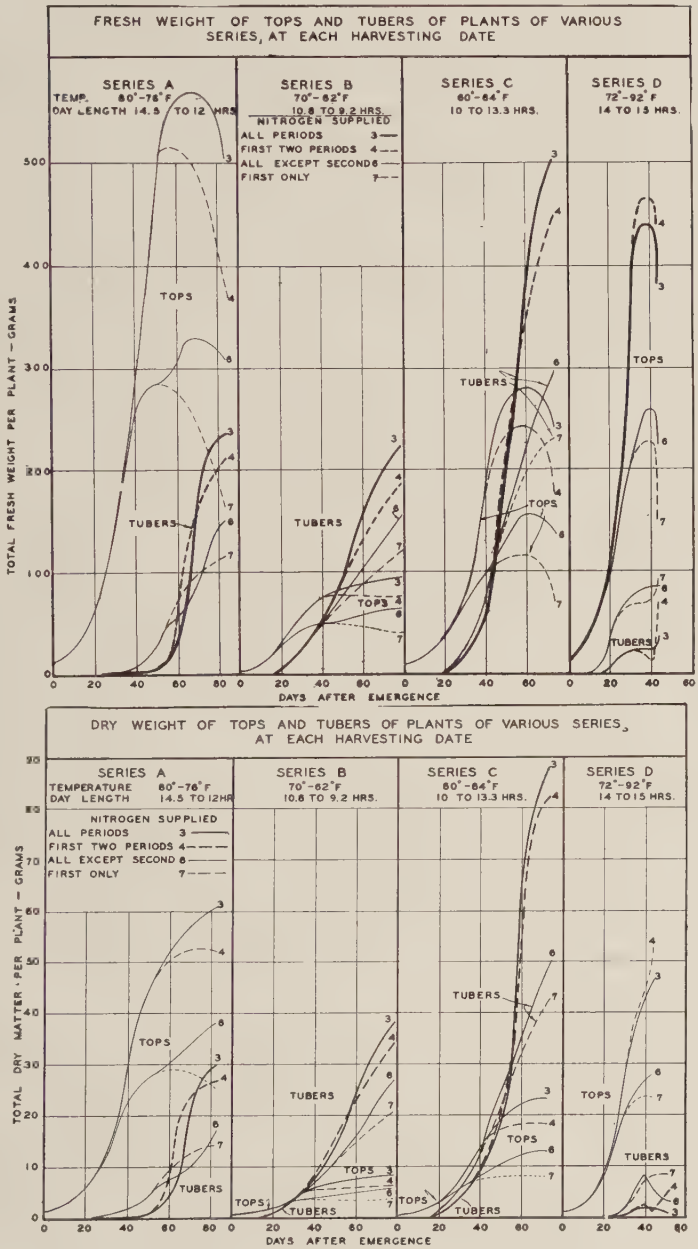
Period when harvested	Series A 80° to 76° F. 14.5 to 12 hours				Series B 70° to 62° F. 10.8 to 9.2 hours				Series C 60° to 64° F. 10 to 13.3 hours				Series D 72° to 92° F. 14 to 15 hours				Series DS[1] 72° to 92° F. 10.5 hours	
(a) MEAN DAILY INCREASE IN GRAMS OF DRY WEIGHT OF TUBERS PER PLANT																		
First	0				0.006				0				0					
Second	0.022		0.144		0.284		0.278		0.37		0.54		0.0		0.073		0.280	0.130
Third	0.61	1.18	0.32	0.43	0.710	0.722	0.420	0.380	2.43	2.42	1.17	1.00	0.24	0.25	0.76	0.65		
Fourth	0.85	0.30	0.59	0.15	0.829	0.644	0.575	0.342	2.27	1.94	1.11	0.82	–.12	–.38	–.68	0.23		
Fifth													–.17	1.39	–.77	0.11		
(b) MEAN DAILY INCREASE IN MILLIGRAMS OF DRY WEIGHT OF TUBERS PER GRAM OF DRY WEIGHT OF LEAVES																		
First	0				1.36				0				0					
Second	1.8		17.3		118		172		71		169		0.0		11.5		42.4	33.9
Third	24.9	49.4	20.8	30.7	153	173	133	157	194	226	166	192	13.3	14.0	66.0	64.3		
Fourth	27.5	12.1	30.2	10.7	144	147	148	127	136	156	118	150	–5.9	–17.0	–49.0	22.4		
(c) MEAN INCREASE IN MILLIGRAMS OF TUBERS (DRY WEIGHT) PER GRAM OF DRY LEAF, PER HOUR OF DAYLIGHT																		
First	0				0.13				0				0					
Second	0.13		1.23		12.0		17.4		6.0		14.3		0.0		0.79		4.05	3.72
Third	1.83	3.77	1.59	2.34	16.6	18.8	14.4	17.0	16.1	18.7	13.7	15.9	0.89	1.00	4.40	4.29		
Fourth	2.21	0.97	2.44	0.87	15.4	15.7	15.8	13.6	10.6	12.2	9.2	11.8	–.39	–1.10	-3.30	1.49		

[1] When calculated for all days of the first and second periods as was done with 2DS, the values for the other series were as follows:
Daily increases per plant: 2B—0.165 gm., 2C—0.197 gm.
Daily increases per gram of dry leaves: 2B—83.2 mgs., 2C—43.8
Increases per gram of dry leaves per hour of daylight: 2B—8.26 mgs., 2C—4.01 mgs.

per plant, while the very small leaf area of the very-short-day plants limited the yield per plant in Series B. The plants of these two short-day series were also the most efficient in building tubers, for they produced more milligrams of tubers per day or per hour per gram of leaves (dry-weight basis) than any other plants, and also had the highest ratio of dry weight of tubers to tops (Table 18). On the basis of hourly production per gram of leaf (dry weight), the short-day plants of Series B were the most efficient. This is of added interest when one considers that the intensity of the light was very low in Series B (Table 1).

The plants of the shortest-day series (B) always had the highest ratio of dry weight of tubers to tops and had the heaviest average daily or hourly production of tubers per gram of leaf during the early part of the season, when these plants were depositing dry matter in tubers as rapidly as or more rapidly than in the tops. During the middle period of most active tuberization the greater average intensity of the light coming to Series C caused those plants to produce the greatest daily increment of tubers per plant and per gram of leaf per day but not quite so much per gram of leaf per hour. This may have been due to the greater efficiency of the reduced light intensity during the winter days, comparable to what has been reported for tomatoes and tobacco (*24*). The brighter illumination of the plants of Series C caused them to mature earlier and consequently during the last period the daily and hourly gain of tubers for a given weight of leaves declined more rapidly in Series C than in B. Series C, with an intermediate day, was still producing more grams of tubers per day because of the larger leaf area, but the leaves were less efficient than those of the short-day series (B), which were showing no signs of maturity of tops. In Series B green weight of tops increased very slowly throughout the experiments, whereas in Series C the period of most active tuberization was followed by a decrease in the green weight of the tops. Most of this decrease occurred in the leaves (Figs. 23 and 24).

The daily increment of tuber production of the 10.5-hour, medium-temperature plants (DS) was actually higher when considering the first two periods as a unit of time than it was for the lower-temperature, short-day plants of Series B and C, the values having been 0.280, 0.165, and 0.197 grams for Series DS, B, and C, respectively. However, as



FIGS. 23 and 24.—Curves of total fresh weight (upper) and dry weight (lower) of the vegetative parts (leaves, stems, and stolons) and tubers of plants grown with each nitrogen treatment in each series (based on data in Tables 4 and 5 respectively).

tuber-producing plants they were actually less efficient than the low-temperature plants, the mean daily production of tubers per gram of leaf figured for the first two periods of DS, B, and C, having been 42.4, 83.2, and 43.8 milligrams respectively (Table 14).

With long warm days earliest tuberization occurred in Series D, but as the season advanced and days got hotter and longer the process was retarded and later there was an actual loss of tuber weight, whereas in Series A, with the days getting shorter and the temperature dropping a few degrees, there were increases in the weight of tubers, in the ratio of tubers to tops, and in the daily or hourly gain of tubers per gram of leaf. Another series (E) grown under day-length conditions comparable to Series A but with higher temperatures, had produced no tubers by the 60th day, when the series was terminated. These long-day, medium-to-high-temperature plants were the least efficient for tuberization.

As the plants of Series D were unavoidably subjected to excessively high and lethal temperatures after the 30th day, the results secured when harvested finally on the 43rd day are of limited value for comparative purposes. However, the tuber/top ratio of the 10.5-hour plants continued much higher than in any of the long-day, high-temperature plants and although the temperature averaged 90° F. for the third period, there was a slight gain in tuber weight instead of a loss.

While the plants of the different series are not strictly comparable because of having been subjected to different light intensities during the photoperiod, these data do indicate that when temperatures are not excessive during the early period of growth a slight shortening of the day (30 minutes to an hour) may be more effective in increasing tuberization efficiency than a considerable drop in temperature (10 degrees F.), and that tuberization will continue for a considerable period with short days in spite of high temperature.

Withholding nitrogen at the end of the first period increased the daily gain in dry weight of tubers per plant during the second period from plants growing with intermediate (C) or long days (A, D) (Table 14). However, with short-day plants (B, DS, ES) the daily increase in dry weight of tubers was less without than with nitrogen. When considering the decreased leaf area resulting from the elimination of the nitrogen supply and then calculating tuber gains per day or hour of daylight on the basis of dry leaf weight, the production of tubers is found to have been in-

creased by nitrogen withdrawal in all except the high-temperature, short-day plants (Series DS).

In all series the total daily tuber production per plant increased more slowly after the initial rapid rise and was lower than with continuous-nitrogen plants (except D). This relative falling behind of minus-nitrogen plants was most apparent in the series with shortest days, and least so with the longest and warmest days. In fact, in Series D, where the days were very long and increasing in length and temperatures were very high, the yield of tubers was increasing constantly in the minus-nitrogen plants, while in the continual-nitrogen series it was decreasing after the 30th day. This decline in daily tuber production per plant was evidently due to the more limited leaf area of the minus-nitrogen, short-day plants.

The tuber production per day or per hour for each gram of leaf in minus-nitrogen plants, although possibly decreasing, continued to be higher than in the continual-nitrogen plants whenever the length of day was increasing (C and D), but when the days were decreasing in length (A and B) the values for the minus-nitrogen plants decreased most rapidly during the last period.

With the high-temperature, 10.5-hour, constant-day-length plants the tuber production was much more rapid, when considered on every basis, than with the long days at the same temperature (5DS compared with 2DS), but at the end of 30 days it was lower than with the continual-nitrogen, 10.5-hour-day plants, instead of higher as in other series. At a date earlier than the 30th day the tuberization rate might have been accelerated by nitrogen withdrawal but apparently the decline which occurred in all series began earlier in this series or was more rapid because of the higher temperature.

This is borne out by the results when short-day, high-temperature plants were harvested at earlier and shorter intervals (ES). On these plants, on which tuberization was just beginning when nitrogen was withheld, tubers grew more rapidly during the next three weeks than on the continual-nitrogen plants, but during the fourth week the tuberization rate fell off rapidly and the minus-nitrogen plants bore a lighter crop of tubers than the continual-nitrogen plants. As was previously reported, none of the long-day plants (E), grown under the same high temperature, produced any tubers (Fig. 22).

Withholding nitrogen at the end of the second period accelerated tuberization to a higher level with long-day, high-temperature plants than that attained by plants of any other

treatment. After this initial period of rapid tuberization there was again a rapid decline in the rate, below that of the continuous-nitrogen plants. With short days the daily increase of tuber weight during the third period was not altered significantly by withholding nitrogen at the end of the second period and although continual withholding reduced the daily increase during the fourth period below that of the second period and below that of continual-nitrogen plants, the reduction was not nearly so great as with long-day, high-temperature plants (Table 14a).

The production of tubers per day or per hour for each gram of dry leaf weight (Table 14b and c) was greatly accelerated in all series during the third period. These rates declined during the fourth period below those of the continual-nitrogen plants with long, warm days (A, D) but not with short, cool days (B, C).

With long, warm days of decreasing length (A) nitrogen withdrawal was followed by an immediate decrease in the green weight of the leaves and stems. The very slight growth of these organs weighed less than did the leaves which died prematurely of starvation (Tables 4 and 5). The brief increase in dry weight of tops was due to differentiation of fibrous supporting tissues and to starch accumulation resulting when less carbohydrate was used in making new tissues. The growth of tubers was greatly accelerated because of the surplus carbohydrate material available which the plants either could not use for new top growth because of an inadequate nitrogen supply or did not need for respiration, and because of the simultaneous accumulation of most of the unassimilated nitrogen into the tubers and the translocation of some assimilated nitrogen from the tops to the tubers. Thus it would seem that when carbohydrates are supplied in abundance, tubers are able to grow when the nitrogen supply is inadequate for the growth of stems and leaves and that as the inorganic supply of nitrogen in the plant decreases the tubers can draw upon nitrogen assimilated in the leaves and stems. As the plants became older and nitrogen starvation more severe, the ratio of the weight of assimilated nitrogen in tubers to that in the tops increased. With this restricted nitrogen condition the percentage of the tuber consisting of nitrogen was less than when it was constantly supplied to the plants.

The reduced rate of tuber growth per gram of leaf in long days was largely due to the reduction in leaf area by the dying of many of the leaves as a result of nitrogen starvation (Table 14). Had this ratio been determined only for the

green or more or less active leaves instead of on the total leaf growth, which included dead and senile leaves, the ratio would not have declined so rapidly. However, as nitrogen was constantly being removed from the upper leaves their activity was reduced and the ratio was actually declining and would have been lower later in the season than that of the continuous-nitrogen plants.

When days were getting longer and hotter (D) there was a brief slight acceleration of tuberization following the withholding of nitrogen. During a period of extremely high temperatures when the leaves of continuous-nitrogen plants were severely damaged, the plants which were not being supplied nitrogen appeared to pass through a hardening process and consequently leaves were more resistant to heat. With the high rate of respiration accompanying the high temperatures, the carbohydrates were used up more rapidly than they were manufactured and some were withdrawn from the tubers, as was also some assimilated nitrogen. After this period the temperature was not quite so high and the minus-nitrogen plants were able to store dry matter in the tubers again, while those supplied with nitrogen continued to lose weight, many of the leaves having been destroyed.

With short days and low temperatures the daily production of tubers per plant did not increase above that of the continuous-nitrogen plants, but the tuberization rate per gram of leaf per day or per hour was higher and although it also decreased with age it continued higher than in the plants of any of the other nitrogen treatments. The difference between these series and the long-day series was that with the short-day plants the green and dry weight of the tops increased very slightly or remained constant but the weight of assimilated nitrogen decreased. The ratio of dry matter and assimilated nitrogen in tubers to tops increased.

With short days and high temperature (DS) the data are incomplete, but tuberization continued in these plants in spite of hot weather, the tuber yield on the 43rd day having been about three times as great as that of comparable full-day plants and twice as great as that of short-day, high-temperature plants receiving nitrogen continually.

It seems that withholding nitrogen was very effective in increasing the tuberization rate. At high temperatures regardless of length of day it also increased the total tuber weight for a period whose duration varied according to conditions. With short days at low temperature the weight per plant was increased only slightly for a very brief period or not at all, but the hourly tuberization rate per unit of leaf

weight was raised to the highest level of all treatments. Withdrawal of nitrogen late in the season increased the yield per plant only under high-temperature conditions, but it raised the tuberization rate to a very high level. With short days at a high temperature, tuber production was greatly increased by nitrogen withdrawal at any time. In all series the tuberization rate declined as the season advanced, because of the decreased activity of all and final death of some of the leaves. In Series X, each time nitrogen was withheld there was a decrease in tuber production (Xa to Xd).

Adding nitrogen after the second period almost always resulted in a lower dry-weight ratio of tubers to tops than occurred in plants with which nitrogen starvation was continued. Immediately after nitrogen was added there was a more or less rapid increase in top growth for a short time, followed by a decrease in the green weight of tops in all except the short-day plants (B, DS) (Figs. 23 and 24). The daily production of tubers per plant was increased promptly by nitrogen addition in all except Series A (Table 14). During the final period of growth the daily tuber production increased still further when days were decreasing in length (A, B) or were continuously short (DS), but when days increased in length (C, D) the daily tuber production per plant was less, actually decreasing with high temperatures and long days (D). The daily increase of tuber weight was greater during the last period than where starvation was continued except when heat was excessive in long days (D). An important observation is that when the temperature was high and days short (DS), tubers were produced at a more rapid rate when nitrogen had been added than when nitrogen starvation was continued. The yield of tubers never became as high as where nitrogen had been supplied during the first two periods except in the long and short day, high-temperature series (D, DS), where the yield of Lot 6 was higher than of Lot 3.

The rate of tuberization per gram of leaf per day or per hour was distinctly lowered during the first period following nitrogen addition (Table 14b and c). When days were decreasing in length (A, B) this rate increased during the final period above both the earlier rate and the rate of all the other treatments of the series, but when days were increasing in length (C, D) the rate was lower than for the previous period or for other treatments of the same series. Factors favorable to tuberization were being brought to bear upon the plants with increasing force with the several minutes cut off the length of each day. These forces may have been the

reduced day length plus reduced light intensity. Not only was the length of day being reduced, but with Series B the intensity of the light was also decreasing, having been about 65 per cent as strong as in Series C during the beginning of the tuberization period, and 55 per cent during the last two periods (Table 1 on gram calories). Thus the decreasing intensity of the light may also have been a factor favoring tuberization. With the shorter day there was more time for carbohydrate translocation.

In the supplemental series (X) plants continuously supplied with nitrogen (Xd4) did not produce the greatest weight of tubers at an early date (Table 12). Maximum early yields were secured from plants deprived of nitrogen during the previous three (Xc4), five (Xb4), or seven (Xa4) weeks, with the one deprived of nitrogen the shortest time yielding most. When nitrogen was supplied to plants, vegetation was stimulated and tuber production was low but later it was increased because of the increased plant size. As a consequence on January 24 plants that never had received any nitrogen (Xh4) produced a greater weight of tubers than those which had received it only during the previous three or five weeks (Xg4, Xf4). However, these minus-nitrogen plants were exhausted and would not have produced appreciably more tuber weight, whereas the tuber weight of those recently receiving nitrogen (Xf5, Xg5) increased greatly during the next 20 days, even though they received no nitrogen during that time.

Number of tubers per plant.—With a continual nitrogen supply the total number of tubers increased steadily throughout the tuberization period (Table 15); the most rapid increase occurred during the first three to six weeks. The number of tubers weighing over one gram advanced very little during the last period. It is not possible to determine definite correlations between tuber number and day length or temperature, but higher temperatures seem to have increased the number, especially when accompanied by a short day (DS).

Withholding nitrogen at the end of the first period tended to increase the number of tubers if tuberization was not yet under way (5A, 5D) and to decrease it where plants were tuberizing rapidly (5B, 5C, 5DS). Under the conditions most favorable for storage of reserve dry matter as in B, C, and DS, a few tubers enlarged quickly and tended to monopolize the flow of reserve material so that other tuber primordia were not enlarged.

TABLE 15.—*Number and size of tubers produced.*

Period after which harvested	Series A 80° to 76° F. 14.5 to 12 hours				Series B 70° to 62° F. 10.8 to 9.2 hours				Series C 60° to 64° F. 10 to 13.3 hours				Series D 72° to 92° F. 14 to 15 hours				Series DS [1] 72° to 92° F. 10.5 hours	
(a) MEAN TOTAL NUMBER OF TUBERS PER PLANT																		
First	0				3.29				0				0					
Second	5.83		3.19		9.10		10.16		8.27		7.75		2.1		9.3		17.5	10.0
Third	8.30	9.00	4.25	4.53	10.4	8.3	8.7	7.2	16.7	18.3	14.4	14.8	8.55	6.78	12.3	10.9		
Fourth	19.50	14.00	7.33	4.67	10.5	13.3	10.7	12.8	18.2	16.0	12.5	16.3	9.66	9.33	8.5	9.2		
Fifth													7.38	9.12	9.6	7.6	18.5	9.7
(b) TUBERS WEIGHING ONE GRAM OR MORE, MEAN NUMBER PER PLANT																		
First	0				0.4				0				0					
Second	1.50		2.13		4.80		4.33		6.56		6.22		0.25		3.25		10.0	6.5
Third	5.75	6.12	3.25	2.63	4.67	4.00	4.50	5.00	6.83	7.00	7.17	6.50	4.22	2.83	6.11	5.89		
Fourth	6.42	6.50	4.00	2.50	5.33	4.83	4.33	4.67	6.67	6.83	7.17	7.29	4.50	2.77	4.17	5.50		
Fifth													5.25	6.52	5.50	5.59	13.5	5.7
(c) MEAN WEIGHT PER TUBER (IN GRAMS) OF TUBERS WEIGHING ONE GRAM OR MORE																		
First	0				1.6				0				0					
Second	2.9		15.0		9.9		10.4		9.9		10.6		1.8		2.2		4.2	4.9
Third	26.7	26.4	24.9	36.1	28.1	30.3	21.2	17.7	53.8	49.6	33.3	28.3	5.0	7.4	12.5	11.0		
Fourth	36.7	32.8	37.5	46.8	43.5	36.6	36.8	26.5	76.2	64.1	43.0	30.2	4.9	4.3	15.7	9.3		
Fifth													5.3	9.1	9.6	6.8	12.6	16.8

[1] Data for 4″ DS and 6″ DS were as follows: (a) 20.5 and 14.3; (b) 12.5 and 9.0; (c) 17.5 and 15.7.

Withholding nitrogen at the end of the second period, when most of the tubers were already established, resulted in a lower number of tubers than where nitrogen was continued if days were short (4B), but with days of intermediate or greater length (4C, 4A, and 4D), there appeared to be an increase in number of tubers, especially those weighing over one gram. In Lot 4D the elimination of nitrogen resulted in a great stimulation of stolon growth, and tuber setting was retarded for a time, but 13 days later the total number of tubers was greater and 23 days later tubers over one gram were more numerous than where nitrogen was continued.

Supplying nitrogen at the end of the second period to starved plants with numerous large tubers may have increased the number of tubers but only very slightly.

In the supplemental series (X) there was an increase in the number of tubers for each additional period during which nitrogen continued to be supplied (Xa3 to Xc3 and Xa4 to Xd4). When nitrogen was withheld at planting time and supplied at a later date, as a general rule the earlier the nitrogen was supplied the greater was the number of tubers. Generally speaking an early nitrogen shortage, especially if prolonged, reduced the number of tubers.

Size of tubers.—With a continual nitrogen supply the increase in mean weight per tuber was very slow when days were long and warm (A and D, Table 15c). The increase in size was accelerated as the days became shorter and cooler during the third period of Series A, in contrast to a questionable increase as the days became hotter and longer in Series D. With the shorter days the tubers were larger at an early date. The tubers of the short-day midwinter series (B) were largest of all at an early age but they did not attain as great size later as did those of the late-winter, short-to-medium-day series (C). This latter series also produced more tubers weighing one gram or more in all of the treatments than did any other series.

The tubers which were set first began to enlarge rapidly. Most of the increase in total tuber weight was due to rapid enlargement of tubers set early and very little to the differentiation of new tubers. As the plants became older the percentage of tubers weighing 25 grams or less remained relatively constant, at 51 per cent of the total number with Series A, 46 per cent with Series B, and 37 per cent with Series C. The late-season increase in percentage of tubers between 10 and 25 grams was the result of very slow growth of many of the smaller tubers (some of which were practically at a stand-still while others were greatly increasing in size), and

also to the swelling of a few primordia into small tubers. When tubers once attained a weight of 25 grams they generally grew rapidly to a greater weight, for the percentage in this size decreased constantly as the season advanced. This was especially the case when conditions for tuberization were best (B and C). With the short-day series, tubers of the larger sizes (over 75 grams) comprised most of the total tuber weight. There was some shriveling of tubers due to resorption, but only in the two lower weight groups (Figs. 19 to 22).

When nitrogen was withheld at the end of the first period a number of tubers quickly increased in size, and the average weight per tuber during the next few weeks was definitely increased. This was most pronounced in Series A (in which storage had been least active), and much less so in Series B (where storage had been most active), while Series C was intermediate but closer to B. As the set of tubers was practically the same as with the continued-high-nitrogen plants, except Series A, and the photosynthetic area did not increase, the number of smaller-sized tubers (10 or 25 to 50 gms.) constituted the greatest percentage of total number of tubers with very few tubers weighing over 75 gms. Only in Series A was the percentage of tubers under 25 gms. less than in the high-nitrogen series at the time of the third and fourth harvesting. In Series A and D the average weight per tuber continued the highest of all treatments throughout the duration of the experimental period. With Series A new tubers were constantly being developed on the high-nitrogen plants, while in Series D the tender leaves were rendered more active by the heat, and tuber weight actually decreased. Apparently termination of vegetative growth resulted in the immediate enlargement of a number of tubers per plant at about an equal rate. This rate could not be maintained by the plants with limited leaf area and consequently as the nitrogen shortage in the tops became more acute fewer of the tubers advanced beyond the smaller sizes and the range of tuber size was thus much less (and size more uniform) than with high nitrogen. Furthermore with an acute nitrogen shortage the nitrogen appeared to have withdrawn from tuber primordia sufficiently to prevent later resumption of growth. The performance of Series A suggests that a somewhat less severe restriction in the nitrogen supply might permit enlargement of more of the tubers, thus producing a crop of uniformly large tubers.

When nitrogen was withheld at the end of the second period there was a tendency toward a higher percentage of

tubers of intermediate size (25 to 75 or 100 gms.) and a lower precentage of very large or very small tubers. There were more tubers of the larger sizes than when nitrogen was curtailed earlier, but the average tuber weight at the end of the season was less than with continuous nitrogen except in the unusual environment of Series D.

Addition of nitrogen to starved plants tended to increase the size of all tubers, so that a higher percentage was found in heavier-weight groups and the average weight per tuber was greater (except Series A) than where nitrogen starvation continued. A number of tuber primordia were brought into the 1-to-10-gram size. The distinct decrease in the percentage of tubers in the 10-to-25-gram size indicates that most of these smaller tubers were being used for the storage of much of the reserve food.

Shape of tubers.—The measurements of all tubers weighing one gram or more fail to reveal any effect of any of the treatments upon the shape of the tubers. Mean ratios of width to length for all tubers of various sizes from the third

TABLE 16.—*Mean of ratios of width to length of all tubers weighing over one gram harvested at the close of the third period in the series enumerated.*

Treatment	Periods when nitrogen was supplied	Series			
		A	B	C	D
3	All	1.158	1.095	1.130	1.120
4	1st, 2nd	1.181	1.095	1.190	1.230
6	1st, 3rd	1.017	1.156	1.200	1.110
7	1st	1.032	1.145	1.190	1.210

harvest of each series are shown in Table 16. In general the tubers grew longer (lower W/L) as they became larger. Consequently the mean W/L ratios for all tubers harvested from restricted-nitrogen plants were sometimes higher than when nitrogen was not restricted. Comparisons of ratios for tubers in the same weight groups fail to reveal any consistent tendencies. This raises a question as to whether differences in shape reported in the literature are due to the nutritional condition of the plant or to the alteration of the physical condition of the soil, which would thus provide differences in physical resistance to tuber expansion.

ROOT GROWTH

Roots generally occurred in groups of five, with sometimes seven, at the various nodes of the subterranean stem and

rarely in groups of three, as stated by Artschwager (*8*). This may be a variety characteristic.

With young plants supplied with nitrogen, the ratio of tops to roots was increased more by long, warm days (D) than by cool, short days (C). However, the high ratio of plants grown with high temperature and a short day (DS) indicates that the short day may have been more responsible for limited root growth than the low temperature (Table 17). As the plants became older the tops grew relatively much more than the roots. The ratios reported in Table 17, which were based on dry weights of washed roots, are very different from the 44:1 stem/root ratio reported by Hosaus, as reported by Artschwager (*8*), or the 2.4:1 top/root ratio reported by Schulze (*106*).

TABLE 17.—*Mean dry weight per plant of roots from plants of three series and ratios of dry weights of tops to those of roots.*

Period after which harvested	Series C 60° to 64° F. 10 to 13.3 hours				Series D[1] 72° to 92° F. 14 to 15 hours			
	Mean dry weight of roots per plant, in grams							
First	0.806				0.883			
Second	1.984		1.332		3.250		4.210	
Third	1.906	1.703	1.333	1.101	5.188	4.902	3.177	2.980
Fourth	2.190	2.079	1.488	1.211	5.250	5.750	6.160	4.160
	Ratio of dry weight of tops to roots							
First	2.76				5.94			
Second	6.75		5.25		9.36		5.06	
Third	11.83	10.74	9.24	7.33	8.26	9.06	8.36	8.06
Fourth	10.95	8.77	8.66	6.75	9.15	10.03	4.57	5.79

[1] Mean dry weight of roots of 2DS was 1.890 gms., of 5DS 1.202 gms. Ratio of tops to roots of 2DS was 10.33 and of 5DS was 8.32.

Withdrawal of nitrogen at the end of the first period generally resulted in a lower weight of roots per plant, but root weight in proportion to the tops was increased as shown by the decreased top/root ratio. After several weeks of nitrogen deficiency the dry weight of roots actually decreased and while the weight may have fluctuated it never became so great as shortly after the nitrogen supply was withheld. The ratio of tops to roots was always less than with plants receiving a continual nitrogen supply. Temperature and day length did not modify the effect of the nitrogen deficiency upon root development. In Series DS, where excessive temperatures caused early death of the plants, the minus-nitrogen, short-day plants had more root weight and more tubers

in relation to tops at the age of 43 days than did continued-nitrogen plants.

Withdrawal of nitrogen at the end of the second period reduced the dry weight of roots, but less so than did the earlier withdrawal. With short days and low temperature (4) the top/root ratio was reduced below that of the continual-nitrogen plants, showing that root growth was affected less than top growth but with long days and high temperature (4D) the top growth was favored more than root growth as the top/root ratio was greater than with the continual-nitrogen plants.

Addition of nitrogen at the end of the second period always increased the weight of roots. This response was greater under high temperature than low temperature when considered either as increased total dry weight or as reduced top/root ratio. The root weight never equaled that of the continual-nitrogen plants. With this treatment roots of a decimeter or more in length were frequently found growing out of tubers just above the eyes, as with the underground stem. This occurred most frequently in Series C.

With well-developed plants in Series C the total top and tuber growth was 51 times heavier than root growth when plants were liberally supplied with nitrogen but when deprived of it for a period of six weeks this ratio dropped to 41.9. With long, warm days the roots constituted a much greater proportion of the total plant weight.

RELATIVE DEVELOPMENT OF VARIOUS PLANT PARTS

The relative development of the vegetative parts or tops [6] as compared with the storage organs or tubers was always greatest with long days and high temperatures, and tuber development was greatest with short days and low temperatures (Table 18). Although the tuber/top ratios (based on dry weight) increased with age in all plants receiving nitrogen continually, the increases were greatest with the shortest days and lowest temperatures. The decreasing ratios of Series D during the last two periods were due to resorption of the tubers during hot weather.

Nitrogen withdrawal at the end of the first period increased the tuber/top ratio most when days were long and warm, but it continued to be higher throughout the life of the plants than when nitrogen was supplied continuously. Withdrawal at the end of the second period resulted in changes of a similar type but to a less pronounced extent.

[6] Refers to total weight of plant less roots and tubers.

TABLE 18.—*Ratios of dry weights of tubers to dry weights of tops at the close of each period.*[1]

Lot number and N treatment each period				
First	(1) +			
Second	(2) +		(5) 0	
Third	(3) +	(4) 0	(6) +	(7) 0
Fourth	(3′) +	(4′) 0	(6′) +	(7′) 0
Fifth	(3″) +	(4″) 0	(6″) +	(7″) 0

Series A				
First	0			
Second	.014		.149	
Third	.321	.429	.269	.424
Fourth	.490	.532	.455	.565

Series B				
First	.096			
Second	1.149		1.790	
Third	2.857	3.448	3.226	4.000
Fourth	4.762	5.556	4.762	5.555

Series C				
First	0			
Second	0.568		1.472	
Third	2.632	3.226	2.857	4.000
Fourth	3.180	4.545	3.846	5.263

Series D				
First	0			
Second	.0004		.051	
Third	.054	.054	.313	.303
Fourth	.040	.022	.211	.344
Fifth	.024	.108	.104	.327

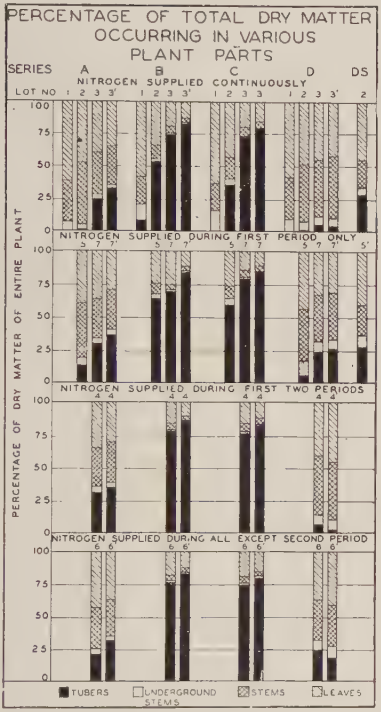
Series DS				
First	No plants harvested			
Second	.444		.380	
Third	None harvested at close of these periods			
Fourth				
Fifth	.378	.736	.768	.559

[1] "Tops" refers to all vegetative parts, total plant except tubers and roots.

Resupplying nitrogen at the end of the second period caused the lowest tuber/top ratio in Series A because of renewed top growth. In all other series it was generally lower than when starvation continued but higher than where N was supplied continuously. The distribution of the total weight into the various plant parts is presented in a graphical manner in Figure 25.

PHYSIOLOGICAL RESPONSE OF PLANTS TO EXPERIMENTAL TREATMENTS

Working along lines suggested by some results from earlier studies by Klebs (*55-58*) on flowering and fruiting, Kraus and Kraybill (*64*) developed principles in relation to fruit production which since then have been repeatedly demonstrated to be essentially correct. They found that the carbohydrate and nitrogen content of the plants was quickly changed by altering the nitrogen supply and that the type of growth and degree of fruiting were correlated with the relationship of these two groups of compounds or their fractions. It has been shown that heat or light may prevent the normal development of tomato flowers (*112* and *128*). This prevention of fruiting then permits a more vegetative type of growth than would otherwise occur, and the development of fruit on a mediumly vegetative plant has been found to check the growth and to alter the composition of the plant until the fruit has ripened (*84-87*).



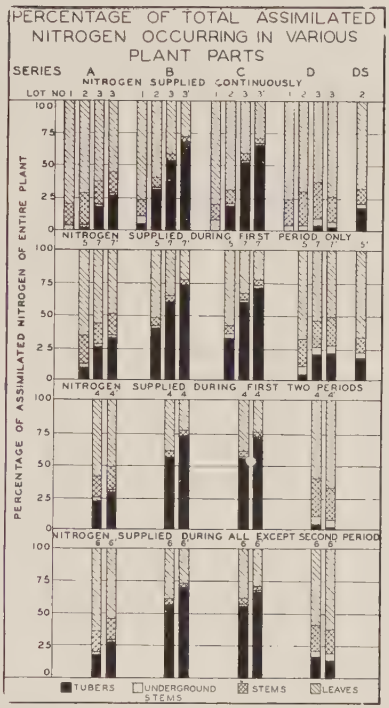


FIG. 25 (left).—Percentage that mean dry weight of each plant part was of the mean total dry weight per plant of all plants harvested at the close of each period, from plants of each series grown with different nitrogen treatments (based on data in Table 5).

FIG. 26 (right).—Percentage that mean weight of assimilated nitrogen located in each of the plant parts was of the mean total weight of assimilated nitrogen in the entire plant, from those harvested at the close of each period, in each series grown with different nitrogen treatments (based on data in Table 24).

The potato tuber is a modified vegetative organ capable of assimilating carbohydrates rapidly in large quantities, thus making it unnecessary or perhaps impossible for the stem and leaves to act as more than temporary storage organs. In order to have a more satisfactory knowledge of the physiological conditions responsible for tuberization and the influence of tuber development upon the vegetative growth it is desirable to have more facts concerning the composition of the potato plant as grown under varied conditions.

PERCENTAGE OF DRY MATTER IN VARIOUS PLANT PARTS

In all series the tubers had the highest dry-matter content, followed by the leaves and stems (except when very

small) (Table 19). The relative amount of dry matter in stolons and stems varied with age and degree of starch accumulation. The dry matter of all vegetative parts tended to increase with age. The larger percentage of dry matter in the vegetative parts of long-day, high-temperature plants may be accounted for by the difference in methods of utilizing carbohydrate reserves. The thickening of cell walls and differentiation of woody tissues were increasing as day length and temperature were increased. Cell walls were thin and there was a minimum amount of woody tissue at a low temperature or with short days. Under long-day, high-temperature conditions carbohydrates that were developed in excess of respiration and growth needs appeared to be used in thickening cell walls and differentiating woody tissues. With short days and low temperatures when cell walls were thin and woody, differentiation was meager and excess carbohydrates were quickly translocated to tubers.

Increasing the carbohydrate content of high-temperature, long-day plants and eliminating carbohydrate utilization in protein synthesis by withholding nitrogen salts increased the dry-matter content still more, as observed at the end of the next period. At the same time it increased the reserve sufficiently so that more of it was translocated and tuberization was accelerated. In contrast to this, withholding nitrogen from short-day or medium-day plants at low temperatures generally reduced the percentage of dry matter in all vegetative parts until the earlier advent of senility. The carbohydrate content was increased for a brief period, as detected by microchemical studies, but with the adequate transportation and storage capacity this small surplus was soon eliminated from the tops so that by the end of the period during which nitrogen had been withheld the plants showed lower dry matter than the plus-nitrogen plants. This was probably due to a decrease in the concentration of the plant solution due to reduced photosynthetic activity, as chlorophyll was breaking down and not being replaced for want of nitrogen which was being absorbed by the tubers.

The addition of nitrogen after it had been withheld decreased the dry-matter content of all vegetative parts when temperature was high and days long (A, D) but actually increased it with very short-day, low-temperature plants (B). Plants from the intermediate-day, low-temperature series (C) had a higher dry-matter content at the end of the next period in the leaves but not in stems and stolons. In Series A and D the resumption of vegetative growth allowed less carbohydrates for differentiation and storage; in Series B and

TABLE 19.—*Dry matter in each plant part as percentage of fresh weight at close of each period.*

Period when harvested	Series A 80° to 76° F. 14.5 to 12 hours				Series B 70° to 62° F. 10.8 to 9.2 hours				Series C 60° to 64° F. 10 to 13.3 hours				Series D 72° to 92° F. 14 to 15 hours				Series DS 72° to 92° F. 10.5 hours	
LEAVES (Data arranged as in Tables 4 and 5)																		
First	10.67				8.69				9.84				11.75					
Second	12.69 10.65		13.25 12.87		9.09		8.76		10.45		9.36		12.66		12.88		11.2	11.7
Third	14.1 22.3	17.4 21.5	14.4 19.0	23.2 34.4	9.76	9.62	9.2	9.0	10.5	9.5	9.8	9.3	14.2	13.8	13.8	16.0		
Fourth	22.6 41.8	42.3 71.0	23.1 27.1	52.6 63.6	9.92	9.42	10.2	11.8	13.6	16.8	12.2	20.0	33.1	29.4	31.0	35.6		
ABOVE-GROUND STEMS, PETIOLES, AND MIDRIBS																		
First	5.70				3.63				3.78 4.52				4.32					
Second	6.82 7.41		6.95 7.83		4.32		4.24		4.26 4.98		4.24 5.14		7.55		8.37		5.77	6.48
Third	5.99 7.55	6.67 7.01	6.77 6.98	6.64 6.98	5.00	4.74	4.60	4.41	5.07	4.75	4.76	5.49	7.3	7.62	7.69	8.1		
Fourth	7.00 7.19	7.70 8.51	7.37 7.57	9.47 9.06	5.33	5.70	5.32	5.27	5.49	5.47	5.13	6.13	11.9	8.29	6.81	11.1		
UNDERGROUND STEMS AND STOLONS																		
First	8.18				6.34				6.10 6.52				6.72 6.15					
Second	12.7		13.9		6.57		7.12		8.16 9.14		8.92 12.16		9.83 8.92		12.3 11.6		8.7 10.7	10.1 12.3
Third	10.4	11.2	11.4	11.8	6.31	6.34	6.84	5.43	9.28 7.94	8.79 7.58	7.45 7.74	7.90 8.25	12.1 8.9	12.2 9.1	11.7 9.9	11.9 9.8		
Fourth	11.3	10.7	11.8	11.1	7.19	6.52	5.88	6.24	8.82 8.51	8.54 7.39	7.99 7.94	7.73 6.99	10.7 8.6	14.6 8.5	10.9 8.4	11.7 9.8		
TUBERS																		
First	0				12.71				0				0					
Second	11.50		12.81		12.67		13.36		13.28		14.97		12.86		13.13		12.2	12.4
Third	11.6	13.6	10.8	12.3	15.1	15.9	14.9	16.0	15.5	16.6	14.9	17.9	10.2 8.2	11.2 9.3	10.9 9.2	11.0 11.2		
Fourth	12.7	12.5	11.5	12.1	16.9	18.2	16.8	16.9	17.5	18.6	16.9	18.4	3.6	6.3	4.9	9.4	7.4	7.4
Fifth																		

C rejuvenation of the weakening leaves increased the concentration of the plant solution. In B the photosynthesis was increased so that there was some starch accumulation in the stems for a considerable period. In Series C this was increased more at first than in B but soon it was almost entirely cleared out by new growth, so that by the end of the third period the stems and stolons of C had the lowest dry-matter content in the series.

The dry-matter percentage of tubers was lowest with high temperatures and long days and highest with low temperatures and short days. With a continual nitrogen supply the dry-matter content increased with age of plants except in Series D, where it decreased because of translocation. Withholding the external nitrogen supply always caused an increase in the percentage of dry matter in the tubers. With plants that were tuberizing rapidly the dry weight of the tubers continued to increase and most of the nitrogen assimilation was in the tubers, and in these tubers the percentage of dry weight continued to increase more rapidly than in the plus-N plants. The plants that were not tuberizing when nitrogen was withheld continued to make their already large tops still larger so that, although tuber growth was accelerated, it soon fell far behind that of the plus-N plants in Series A and the dry-matter percentage decreased. With long days not so warm at the time of nitrogen withholding, the great amount of starch that accumulated (pages 115-119, Figs. 28 and 30) permitted tuber weight to increase quickly and then very slowly as the heat became excessive (D). During all of this time the dry matter was decreasing in the tubers and in the underground stems and stolons of these plants. This was probably because of the great demands for carbohydrates to maintain the large tops under high respiration conditions. As it has been repeatedly shown that the respiration of potato tubers is greatly increased by raising the temperature (*75, 50, 59*), the loss from the tubers in this manner was evidently great enough to accelerate the reduction of the dry matter of tubers of starved plants.

Supplying nitrogen to starved plants decreased the dry-matter content of tubers in all series, so that it was lower than that of the tubers of the continual-nitrogen plants. The percentage increased in all series after this initial rapid decrease.

NITROGEN ABSORPTION

Inorganic forms of nitrogen—nitrates, nitrites, and ammonia—while they may exert some effect on the plant processes by altering the osmotic concentration of the cell sap, are generally not considered as being associated with the life processes of the plant because they have only been absorbed by and have not been assimilated into the compounds that make up the protoplasm and plant structure.

An abundance of inorganic nitrogen, especially as nitrate, may indicate that it is being absorbed in excess of the needs of the plant or of the ability of the plant to utilize it in building organic compounds required for growth. Ammonium may occur as a degradation compound but it seems that nitrates are not formed in the plant in this way (*33*). This inability to utilize nitrates may be due to the shortage of carbohydrates, which are also essential for building organic nitrogen compounds (*64, 89-92*), or it may be due to the inability of the plant to reduce the nitrates (*35*) because of insufficient light, improper temperature, or the deficiency of some element essential for the activity of the reducing substance (*34, 35*).

Inorganic nitrogen.—The data in Tables 20 and 21 reveal that ammonium nitrogen was present in relatively small but reasonably constant amounts. There is no evidence of a greater abundance of ammonium in plants to which ammonium sulphate was supplied in the nutrient solution (C, D) than where it was not used (A, B). Nitrate nitrogen varied a great deal in the various parts and treatments.

When plants were receiving nitrogen salts continually, the percentage of inorganic nitrogen was highest in the stems and lowest in the tubers. In the stems there was a decreasing gradient from midribs and petioles—through stems, underground stems and stolons. The percentage decreased in the vegetative parts as the plants became older and in tubers when days were decreasing in length, but it increased in the tubers produced when day length was increasing.

During short days with either low (B, C) or high (DS) temperatures, the percentage of nitrate or of total inorganic nitrogen was much higher in all plant parts (especially in stems) than with long days and high temperatures, indicating that it was not being assimilated.

Withholding nitrogen resulted in a greatly reduced content of inorganic nitrogen in all plant parts. Most of the decrease was in the nitrate nitrogen. The decrease was relatively greatest in stems. Microchemical tests (page 94) showed this deficiency to have been apparent within five to

TABLE 20.—*Total inorganic and nitrate nitrogen in each plant part as percentage of dry weight.*

PART I—TOTAL INORGANIC NITROGEN

Period when harvested	Series A 80° to 76° F. 14.5 to 12 hours				Series B 70° to 62° F. 10.8 to 9.2 hours				Series C 60° to 64° F. 10 to 13.3 hours				Series D 72° to 92° F. 14 to 15 hours				Series DS 72° to 92° F. 10.5 hours	
LEAVES [1]																		
First	.744				.548				.620				.273					
Second	.144 .199		.054 .060		.468		.127		.360		.090		.158		.091		.215	.112
Third	.292 .178	.101 .092	.132 .144	.092 .084	.461	.118	.437	.089	.289	.099	.242	.077	.220	.130	.225	.073		
Fourth	.144 .169	.083 .077	.165 .200	.078 .078	.366	.074	.317	.083	.231	.089	.190	.074	.444	.167	.272	.094		
ABOVE-GROUND STEMS, PETIOLES, AND MIDRIBS [1 2]																		
First	2.410				2.380				3.510 2.680				2.146					
Second	.519 .459		.079 .013		2.340		.298		2.88 2.30		0.120 0.080		.626		.054		1.09	.130
Third	.488 .430	.260 .155	.319 .276	.050 .053	1.98	.300	1.11	.069	1.62	.177	.755	.039	0.56	.192	.320	.050		
Fourth	.395 .550	.094 .150	.358 .419	.064 .059	1.66	.057	1.28	.090	1.42	.081	.858	.113	1.06	.166	.594	.157		
UNDERGROUND STEMS AND STOLONS [3]																		
First	1.09				1.280				1.673 0.340				0.145					
Second	.210		.059		1.032		.230		1.200 0.634		0.110 0.060		.344 .099		.069 .088		.549	.194
Third	.228	.115	.180	.055	Included with above-ground stems				.654	.140	.414	.040	.310 .370	.093 .062	.162 .268	.058 .033		
Fourth	.219	.079	.244	.091					.629	.085	.441	.089	0.50 1.19	.108 .106	.310 .645	.065 .067		

TUBERS																		
First	0				.102				0				0					
Second	.078		.081		.164		.084		.180		.043		.068		.087		.252	.108
Third	.139	.082	.248	.046	.216	.099	.192	.077	.187	.070	.192	.047	.157	.126	.070	.052		
Fourth	.131	.065	.216	.115	.167	.054	.134	.036	.207	.053	.202	.029	.243	.127	.176	.076		
PART II—NITRATE NITROGEN ONLY [4]																		
LEAVES [1]																		
First	0.712				0.510				0.590				0.211					
Second	.113 .180		0.024 0.044		.430		.095		.320		.060		.075		.033		.139	.048
Third	.148 .150	.059 .067	.104 .104	.043 .053	.424	.088	.397	.058	.247	.066	.187	.040						
ABOVE-GROUND STEMS, PETIOLES, AND MIDRIBS [1 2]																		
First	2.366				2.324				3.430 2.620				0.199					
Second	.485 .432		0.0530 0.0106		2.284		0.278		2.820 2.240		0.100 0.060		.524		0.032		1.00	.104
Third	.464 .412	.120 .141	.294 .246	.032 .041	1.92	.280	1.05	.047	1.48	.160	.670	.015						
UNDERGROUND STEMS AND STOLONS [3]																		
First	1.065				1.178				1.63 0.31				0.891					
Second	.193		0.046		1.012		0.214		1.160 0.610		0.90 0.04		0.297 0.033		0.036 0.055		.486	.161
Third	.196	.086	.160	.041	In with top stems				.550	.120	.290	.206						
TUBERS																		
First	0				0.074				0				0					
Second	.062		0.051		0.108		0.056		0.120		0.030		0.026		0.063		.144	.072
Third	.077	.041	.175	.046	.116	.062	.110	.057	.097	.040	.087	.030						

[1] With data on both lines, in Series A, upper line is for top halves, lower line for lower halves of plant.
[2] With data on both lines, in Series C, data for petioles and midribs on upper line, stems on lower.
[3] In Series C and D when data appear on two lines, upper line for underground stem only and lower line for stolons only.
[4] Nitrate nitrogen was not determined separately in material harvested at close of third period in Series D or at close of fourth period in all series when only total inorganic nitrogen was determined as given in Part I of this table.

TABLE 21.—*Total inorganic and nitrate nitrogen as milligrams of nitrogen per gram of fresh weight.*

PART I—TOTAL INORGANIC NITROGEN

Period when harvested	Series A 80° to 76° F. 14.5 to 12 hours				Series B 70° to 62° F. 10.8 to 9.2 hours				Series C 60° to 64° F. 10 to 13.3 hours				Series D 72° to 92° F. 14 to 15 hours				Series DS 72° to 92° F. 10.5 hours	
LEAVES [1]																		
First	.794				.476				.610				.321					
Second	.1826		.0716		.426		.1113		.3762		.0843		.2002		.1167		.241	.131
	.2120		.0772															
Third	.412	.176	.190	.214														
	.396	.198	.274	.289	.450	.114	.404	.080	.303	.094	.237	.072	.312	.179	.312	.117		
Fourth	.325	.351	.381	.411														
	.707	.547	.541	.497	.363	.070	.322	.098	.314	.146	.232	.148	.728	.490	.845	.334		
ABOVE-GROUND STEMS, PETIOLES, AND MIDRIBS [1 2]																		
First	1.375				.864				1.327 1.212				.926					
Second	.354		.0549		1.011		.1263		1.226		.0509		.480		.0451		.629	.084
	.340		.0102						1.146		.0411							
Third	.292	.174	.216	.037														
	.325	.109	.193	.037	1.01	.150	.537	.032	.820	.084	.359	.021	.411	.146	.247	.040		
Fourth	.277	.072	.263	.061														
	.396	.128	.317	.054	.926	.033	.681	.048	.780	.044	.441	.069	1.26	.138	.405	.173		
UNDERGROUND STEMS AND STOLINS [3]																		
First	.891				.766				1.020 0.222				.942					
Second									.9780		.0982		.3380		.0848			
	.267		.0756		.678		.164		.5796		.0730		.0882		.1022		.533	.213
Third					Included with the above-ground stems[3]								.375	.114	.189	.069		
	.238	.130	.206	.065					.566	.113	.317	.032	.329	.056	.265	.032		
Fourth													.533	.158	.333	.076		
	.246	.085	.288	.101					.547	.075	.351	.066	1.03	.091	.544	.066		

TUBERS																		
First	0				.130				0				0					
Second	.0895		.1038		.208		.112		.239		.064		.0876		.1150		.308	.134
Third	.162	.112	.267	.057	.326	.159	.286	.123	.290	.117	.286	.083	.161	.141	.076	.057		
Fourth	.166	.081	.249	.140	283	.098	.226	.061	.363	.099	.340	.053	.200	.119	.161	.085		
PART II—NITRATE NITROGEN ONLY [4]																		
LEAVES [1]																		
First	.759				.443				.580				.248					
Second	.143 .192		.0318 .0567		.391		.083		.335		.056		.095		.043		.128	.056
Third	.209 .341	.103 .144	.149 .198	.099 .100	.414	.098	.367	.052	.259	.062	.183	.037						
ABOVE-GROUND STEMS, PETIOLES, AND MIDRIBS [1 2]																		
First	1.348				.846				1.297 1.182				.660					
Second	.331 .320		.0368 .0083		.986		.118		1.200 1.112		.047 .031		.395		.027		.577	.066
Third	.277 .311	.039 .047	.199 .172	.021 .029	.960	.133	.516	.022	.751	.076	.344	.008						
UNDERGROUND STEMS AND STOLINS [3]																		
First	0.872				.747				.994 .202				.059					
Second									.947		.080		.292		.0444			
Third	.241		.0641		.673		.153		.557		.049		.0295		.0638		.428	.155
	.204	.097	.183	.048	In with top stems				.047	.092	.226	.016						
TUBERS																		
First	0				.0941				0				0					
Second	.0713		.0653		.137		.0748		.1595		.032		.0345		.0946		.176	.089
Third	.089	056	.202	.051	.176	.098	.164	.091	.150	.067	.130	.045						

[1] With data on both lines, in Series A, upper line is for top halves, lower line for lower halves of plants.
[2] With data on both lines, in Series C, data for petioles and midribs on upper line, stems on lower.
[3] In Series C and D when data appear on two lines, upper line for underground stem only and lower line for stolons only.
[4] Nitrate nitrogen was not determined separately in material harvested at close of third period in Series D or at close of fourth period in all series when only total inorganic nitrogen was determined as given in Part I of this table.

seven days, while at the time the first samples were taken for macroanalysis extremely weak diphenylamine tests were secured. As nitrogen starvation persisted during the third period, the decrease generally continued at a reduced rate with little change during the fourth period, when plants were becoming senile.

When nitrogen salts were withheld at the end of the second period, reductions in inorganic nitrogen were not quite so great relatively as when withheld earlier. This was probably due partly to the decrease accompanying increase in age of continual-nitrogen plants. Percentages in these starved plants were very much the same in all series, but they may not have occurred quite as rapidly with short-day plants. Resupplying nitrogen salts to starved plants at the end of the second period increased the percentage of inorganic nitrogen to about the same level as in those receiving it continuously. Determinations on roots of Series C and D showed a higher inorganic nitrogen content (dry basis) than in leaves when nitrogen was being supplied and a lower percentage when it has been withheld, the latter indicating more rapid depletion of the roots.

Microchemical observations of changes in nitrate content.—All parts of the plants continuously supplied with nitrogen gave a positive test for nitrates, with diphenylamine, until the plants started to mature. Strongest tests were secured in the aerial stems, especially in the stem tips. The tests in underground stems were weaker than in the basal part of the surface stems. Tubers gave lighter tests than stems, and stolons gave the weakest tests of all parts. The tests with the short-day or low-temperature plants were definitely stronger than those with the long-day or high-temperature plants. These tendencies were all borne out quantitatively by the macrochemical determinations.

When nitrogen was withheld at the end of the first period in Series A, weaker nitrate tests were secured in the upper parts of the stem within five to seven days. After 12 days there was a pronounced deficiency in nitrates throughout the entire plant. At the end of 18 days tests were secured only in the top 10 centimeters of the aerial stem and a week later practically none any place. Nitrates disappeared more quickly during the long, warm days than in the short, cool days, but the general order of disappearance was the same. Starch congestion in stems increased before greatly reduced nitrate tests were secured (pages 115-119).

When nitrogen was withheld at the end of the second period, the same type of nitrate deficiencies were found in

about one-half or one-third the time required with younger plants. Supplying nitrogen to starved plants resulted in a great increase in nitrate nitrogen within two days in the upper stem, in all parts in 12 days, while by 20 days the amount was apparently as great as in the continual-nitrogen plants.

ASSIMILATION OF NITROGEN

Assimilated nitrogen may also be considered as total organic nitrogen, to distinguish it from total inorganic nitrogen, since it is the total amount of nitrogen found after ammonia, nitrites, and nitrates have been extracted. Thus it includes nitrogen in all stages of assimilation from the early soluble and mobile forms to the final insolube forms which cannot be translocated without hydrolysis. Undoubtedly the nitrogen fractions included under it are very different in young plants or short-day plants as compared with old plants or long-day plants. In the younger plants much of it is found in the meristematic points where it aids in the development of new tissues, but in the older plants it constitutes a definite part of the more or less permanent protoplasmic structure necessary for the normal functioning of the plant. When it is diverted from this function the life processes of the plants may be greatly altered.

Relation of assimilated nitrogen to total nitrogen content.—The assimilated or organic nitrogen percentage was low in the stems and much higher in the leaves, being just the opposite of the very low percentage of inorganic nitrogen in the leaves and high percentage in the stems (Tables 22 and 23 compared with 20 and 21). In the leaves the assimilated nitrogen constituted between 90 and 92 per cent of the total nitrogen in short-day, low-temperature plants (B) and increased to 93 to 97 per cent in the long-day, higher-temperature plants of Series A and D. In the stems only 50 per cent of the total nitrogen was in the assimilated form in Series B, compared with around 75 to 78 per cent in Series A and D. The importance of high temperature in nitrogen assimilation is shown in Series DS, where the highest percentage of the total was assimilated in spite of a short day. In the tubers there was a tendency for assimilated nitrogen to comprise a low percentage of the total nitrogen with short-day conditions and in all series the percentage of nitrogen that was assimilated decreased as the season advanced.

When nitrogen was withheld at the close of the first period, the percentage of the total nitrogen assimilated was increased in all series to an apparently constant level of 97

to 98 per cent in leaves and 90 to 95 per cent in stems. It was also increased in tubers, but less uniformly so.

When nitrogen was supplied at the close of the second period to starved plants, the percentage of the total nitrogen that was in assimilated form was higher than with continual-nitrogen plants and lower than in the starved plants. The high percentage of unassimilated nitrogen in the short-day, low-temperature series indicates why the plants of these series (B, C) failed to develop extensive amounts of leaves and stems.

Assimilated nitrogen in various plant parts.—There has been very little investigation of the nitrogen content of the various vegetative parts of the potato plant. Wilfarth, Romer, and Wimmer (*136*) reported the highest percentage of total nitrogen in the leaves, followed by petioles, stems, roots, and finally the lowest percentage in the tubers. In all parts the percentage decreased with age, except for a rapid increase in the tubers during the period of maturation. The increase in total nitrogen at this time very possibly may have consisted largely of inorganic nitrogen absorbed by the tubers when plant tops were not synthesizing nitrogen compounds. They found little difference in the nitrogen content of tubers of different sizes except that it was slightly higher in tubers weighing less than five grams. They included the stolons with tubers in the analysis.

Calculating on a dry basis, Appleman and Miller (*5*) found the percentage of total N in tubers, grown in Maryland, fairly constant at all stages of development. The percentage of nonprotein and amino nitrogen increased with increasing periods on the vines. Willaman and West (*137*) reported a higher nitrogen content in potatoes raised in southern compared with northern Minnesota, and also that those grown on clay soils had least nitrogen. Goldthwaite (*44*) found that as potatoes were grown at higher and cooler altitudes the nitrogen content decreased and that irrigated potatoes had slightly less than dry-land potatoes and that numerous irrigations tended to decrease slightly the nitrogen content, as did also production on the heavier soils. Werner (*133*) also reported reduced nitrogen content in irrigated and in straw-mulched tubers, and a lower amount in immature than in mature tubers.

Weigert and Stiehr (*129*) found that potatoes growing on nitrogen-deficient soils had not only a reduced percentage of assimilated nitrogen but also a decidedly lower percentage of amino nitrogen than when farm manure or nitrogen fertilizers were applied. Gericke (*43*) reports a conclusion

which is significant in this investigation, that in wheat high protein content can be secured by supplying nitrogen during the late growth period of the plant or by curtailing excessive grain production which may result from applications of nitrogen early in the season. Berkner and Schlimm (*11a*) report increased protein content in tubers as the applications of calcium nitrate fertilizer were increased in amount.

In this investigation the leaves always contained the highest percentage of assimilated nitrogen when calculated on either the fresh or dry basis (Tables 22 and 23). The stems generally had the lowest percentage with tubers having an intermediate value. The percentage in underground stems and stolons was more similar to that of the tubers than of the aerial stems.

The assimilated nitrogen percentage of leaves and stems was highest in the short-day plants (B, C, DS) on the dry-weight basis, but on the fresh-weight basis it was consistently higher in the long-day, high-temperature plants (A, D). The nitrogen content of the tubers acted in reverse order, the highest percentage occurring in the short-day plants if figured on the fresh-weight basis, whereas on the dry-weight basis the highest percentage occurred in the long-day plants. In Series C during the last period, when the days averaged 12.8 hours in length, the percentage was high on either basis.

As the plants became older there was a general tendency for the percentage of assimilated nitrogen to decrease in all parts except the tubers. There it decreased for a brief early period and then increased steadily until the plants were mature, except in the set grown in long days and abnormally high temperatures (D), where it decreased. The very great increase in nitrogen percentage during the last period in the leaves of all series except B was due to the death of many leaves and consequent increase in percentage of dry matter. Nitrogen in these dead areas could not be translocated.

Withholding nitrogen at the end of the first period was quickly followed by a greatly decreased and continually decreasing percentage of assimilated nitrogen in all parts of the plant. With age the trend was in the same direction as in continuous nitrogen plants. When nitrogen was withheld at the end of the second period the assimilated nitrogen content of all plant parts was also reduced but generally not to as low a percentage as where nitrogen starvation occurred earlier and was more prolonged.

When nitrogen was supplied to plants at the end of the second period, after two or three weeks of starvation, the nitrogen content was greatly increased. Sometimes at the

TABLE 22.—*Assimilated nitrogen in each plant part as percentage of dry weight.*

Period when harvested	Series A 80° to 76° F. 14.5 to 12 hours				Series B 70° to 62° F. 10.8 to 9.2 hours				Series C 60° to 64° F. 10 to 13.3 hours				Series D 72° to 92° F. 14 to 15 hours				Series DS 72° to 92° F. 10.5 hours	
LEAVES (Data arranged as in Tables 20 and 21)																		
First	5.161				5.49				6.45				6.18					
Second	4.87		3.61															
	3.70		2.79		5.47		4.59		5.69		4.52		4.86		3.29		5.07	4.02
Third	4.46	3.83	3.86	3.07														
	3.33	2.99	3.13	2.58	4.98	4.22	4.55	3.70	5.00	3.99	4.62	3.24	4.79	3.82	4.60	2.95		
Fourth	3.82	3.44	3.43	3.04														
	3.19	2.96	3.52	2.71	4.26	3.08	4.05	2.92	4.30	2.66	4.19	2.47	4.94	4.25	4.10	2.75		
ABOVE-GROUND STEMS, PETIOLES, AND MIDRIBS																		
First	1.99				2.60				2.78				2.94					
									3.13									
Second	1.80		1.18						2.14		1.48							
	1.08		0.87		2.43		1.64		2.04		1.34		2.02		1.08		1.81	1.19
Third	1.58	1.35	1.45	1.02														
	1.23	0.97	1.12	0.85	1.98	1.54	1.84	1.37	1.80	1.22	1.85	1.18	2.02	1.66	1.61	1.02		
Fourth	1.40	1.09	1.32	0.97														
	1.23	1.10	1.14	0.82	1.61	1.17	1.61	1.29	1.74	1.06	1.90	1.22	1.97	1.50	1.67	1.06		
UNDERGROUND STEMS AND STOLONS																		
First	1.70				2.07				2.15				1.95					
									3.88									
Second									1.43		1.19		1.76		1.10			
	1.41		1.15		1.74		1.53		1.94		1.26		2.14		1.32		1.75	1.30
Third													2.21	1.79	1.57	1.28		
	1.34	1.22	1.42	1.19	Included with above-ground stems				1.80	1.37	1.61	1.20	2.05	1.82	1.56	1.29		
Fourth													2.20	1.89	1.86	1.31		
	1.37	1.21	1.38	1.13					1.66	1.31	1.67	1.09	1.77	1.79	1.52	1.28		
TUBERS																		
First	0				2.16				0				0					
Second	2.05		1.22		1.81		1.35		1.83		1.11		2.23		1.63		2.01	1.59
Third	1.86	1.49	2.03	1.49	1.73	1.31	1.60	1.17	1.74	1.18	1.71	0.98	2.32	1.74	1.78	1.56		
Fourth	1.89	1.63	2.05	1.50	1.69	1.15	1.72	1.17	1.91	1.12	1.88	0.97	2.33	2.17	2.08	1.41		
ROOTS																		
Third									2.15	2.37	2.16	2.07						

Period when harvested	Series A 80° to 76° F. 14.5 to 12 hours				Series B 70° to 62° F. 10.8 to 9.2 hours				Series C 60° to 64° F. 10 to 13.3 hours				Series D 72° to 92° F. 14 to 15 hours				Series DS 72° to 92° F. 10.5 hours	
LEAVES (Data arranged as in Tables 20 and 21)																		
First	.552				.477				.634				.726					
Second	.617 .394		.478 .343		.497		.402		.595		.424		.616		.424		.569	.469
Third	.627 .742	.665 .612	.552 .596	.313 .317	.486	.406	.421	.334	.524	.378	.453	.302	.679	.528	.553	.472		
Fourth	.862 1.34	1.47 2.10	.793 .952	.295 .331	.423	.290	.412	.345	.584	.446	.512	.493	1.64	1.25	1.27	.978		
ABOVE-GROUND STEMS, PETIOLES, AND MIDRIBS																		
First	.287				.094				.105 .142				.127					
Second	.123 .080		.082 .068		.105		.070		.091 .102		.063 .069		.153		.091		.104	.077
Third	.095 .093	.090 .068	.098 .078	.068 .059	.101	.077	.088	.063	.091	.058	.088	.065	.147	.127	.124	.082		
Fourth	.098 .089	.084 .094	.097 .086	.092 .074	.090	.068	.087	.071	.095	.058	.098	.075	.234	.124	.102	.118		
UNDERGROUND STEMS AND STOLONS																		
First	.139				.131				.126 .245				.129					
Second	.179		.160		.113		.109		.185 .177		.094 .156		.173 .190		.136 .154		.172	.137
Third	.140	.136	.162	.141	Included with above-ground stems				.151	.114	.123	.097	.249 .197	.214 .163	.136 .204	.107 .176		
Fourth	.155	.130	.163	.125					.144	.105	.105	.080	.188 .189	.262 .162	.165 .158	.122 .156		
TUBERS																		
First	0				.2745				0				0					
Second	.2357		.1563		.2292		.1805		.2431		.1663		.287		.2141		.227	.186
Third	.216	.203	.220	.184	.261	.208	.238	.187	.270	.196	.254	.175	.237	.226	.193	.172		
Fourth	.240	.204	.236	.182	.286	.210	.290	.198	.335	.209	.317	.178	.192	.204	.192	.156		

time of the final harvest it was equal to or slightly higher than in the continuous-nitrogen series. Undoubtedly the newer stems and leaves did have a higher nitrogen content but as they were not analyzed separately the increase is not apparent in the data.

Distribution of assimilated nitrogen into various plant parts.—With a continuous supply of nitrogen available the greatest portion of assimilated nitrogen in young plants was located in the leaves (Table 24, Fig. 26). As the plants became older the nitrogen in the leaves constituted a constantly decreasing percentage of the total; that of the stem was also decreasing but the amount in the tubers was greatly increasing. The nitrogen distribution (Table 24) follows in a general way the dry-matter distribution (Fig. 25) except that with the dry matter a higher percentage is located in the tubers and stems and less in the leaves than in the case of assimilated nitrogen.

When days were long and warm the percentage occurring in the leaves was very large and in the stems also relatively high, while the percentage in the tubers was quite small. With short days or low temperatures the nitrogen in the leaves constituted a rapidly decreasing portion of the total. Within five or six weeks after emergence over half of the total nitrogen was in the tubers, an almost inconsequentially small percentage in the stems, and much less than half in the leaves. Stated in another way, with the long days of Series A the ratio of assimilated nitrogen in tubers to nitrogen in the tops was only 0.36:1, but with the intermediate days of Series C it was 1.96:1, and with the short days of B, 2.19:1. The trend toward nitrogen accumulation by the tubers as plants became older was most pronounced in the short-day plants (Fig. 27).

When nitrogen was withheld from young plants the shift of nitrogen from tops to tubers was greatly accelerated but again occurred to a more pronounced degree in the short-day plants (Fig. 27, Table 24). Withholding nitrogen from older plants brought about the same type of changes but with greater rapidity because of the greatly accelerated tuber growth.

Addition of nitrogen to the nutrient solution of starved plants resulted in a slight shift toward the leaves but the percentage of the total nitrogen in the tubers remained slightly greater than where nitrogen was continually available.

Time of nitrogen assimilation.—Liebscher (*68*) critically reviewed the work of numerous German investigators who

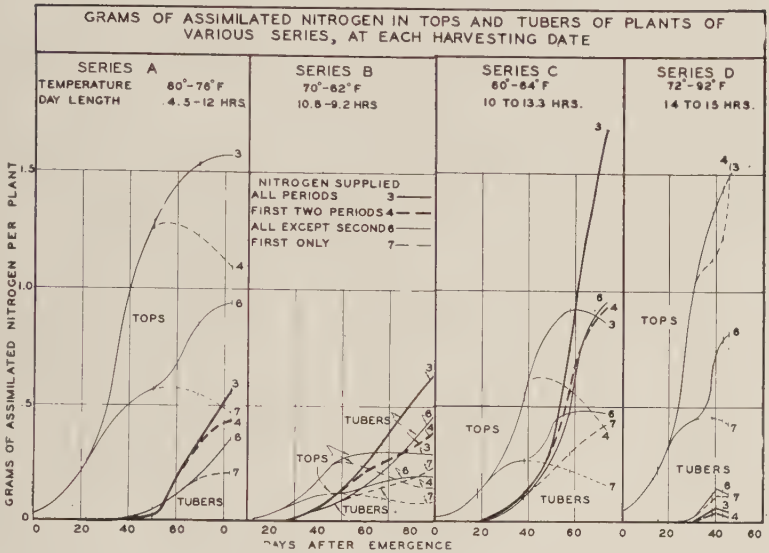


FIG. 27.—Curves showing amount of assimilated nitrogen found during the growing season in vegetative parts (leaves, stems, and stolons) and tubers of plants grown with each nitrogen treatment in each series. (Based on data in Table 24.)

had studied the intake of the mineral elements that were considered as exerting a limiting influence upon the development of the potato plants. From their work, especially that of Kellerman, he concluded that the life of the potato plant could be divided into four major periods. During the first period of five or six weeks, growth is mostly at the expense of the material stored in the mother tuber but the intake of nitrogen and other minerals is active. The second period, prior to blooming, is one of active organic-matter building but the intake of minerals is not increased. With the advent of the third or flower and fruiting period, he reports a brief check in growth, followed by the resumption of the normal rate and an acceleration of organic matter manufacture but with mineral intake decidedly slower. During the final or tuber building period, there is, he reports, little increase in organic matter but active translocation of it from vines to tubers with an increase in the rate of absorption of nitrogen and other minerals, especially of phosphorus.

Wilfarth, Romer, and Wimmer (*136*) reported that in the potato not only did the total weight of the plant increase up to the last harvest but that the total amount of nutrients

TABLE 24.—*Milligrams of assimilated nitrogen per plant in each plant part.*

Period when harvested	Series A 80° to 76° F. 14.5 to 12 hours				Series B 70° to 62° F. 10.8 to 9.2 hours				Series C 60° to 64° F. 10 to 13.3 hours				Series D 72° to 92° F. 14 to 15 hours				Series DS 72° to 92° F. 10.5 hours	
LEAVES [1]																		
First	212				48.3				91.60				173.7					
Second	599		277		216		108		512		224		724		323		621	240
	336		135															
Third	883	668	499	274	264	186	157	92	803	498	420	176	896	745	525	305		
	322	266	170	150														
Fourth	966	632	506	235	265	136	176	81	748	329	411	134	990	1075	588	277		
	219	160	205	99														
ABOVE-GROUND STEMS, PETIOLES, AND MIDRIBS [1 2]																		
First	42				8.3				7.40 6.16				44.6					
Second	183		68		28.4		12.6		42.4		15.5		271.2		97.0		105	41
	130		66						31.3		9.6							
Third	179	148	97	60	33.8	24.0	19.1	12.6	99.4	58.4	45.7	23.5	397	353	175	114		
	157	96	75	54														
Fourth	216	153	114	63	30.4	21.5	20.6	13.2	98.2	53.1	45.4	25.0	457	377	178	118		
	138	115	79	45														
UNDERGROUND STEMS AND STOLONS [3]																		
First	8.3				3.7				5.81 2.72				9.1					
Second	29.9		20.0		4.9		4.1		8.58 6.21		5.80 5.00		22.7 17.6		15.1 15.1		27	16
Third	35.4	45.7	26.3	17.6	Included with the above-ground stems				17.1	12.6	12.6	7.8	36.1 24.8	35.3 30.1	17.4 23.1	13.6 19.2		
Fourth	28.6	32.4	26.4	18.4					15.6	11.8	11.5	7.4	32.2 33.4	50.5 34.0	23.6 28.1	13.3 15.9		

	TUBERS																	
First	0				2.8				0				0					
Second	13.1		50		112		82.4		138		123		1.6		17.8		157	61
Third	335	334.5	183.6	180.2	346.0	265.2	228.6	158.3	1022	691	608	314	53.4	41.8	148.0	113.5		
Fourth	564	434.0	354.0	212.3	647.0	396.1	463.1	246.2	1686	936	940	413	43.8	23.7	123.4	114.0		
	TOTAL IN VEGETATIVE PARTS																	
First	262.3				60.3				113.69				227.4					
Second	1277.9		566		249.3		124.7		600.49		259.9		1035.5		450.2		753	297
Third	1533.2	1223.7	867.3	556.0	297.8	210.0	176.1	104.6	919.5	569.0	478.3	207.3	1353.9	1163.4	740.5	451.8		
Fourth	1567.6	1092.4	930.4	460.4	295.4	157.5	196.6	94.2	861.8	393.9	467.9	166.4	1502.6	1536.5	817.7	424.2		
	TOTAL IN ENTIRE PLANT (EXCEPT ROOTS)																	
First	262.3				63.1				113.69				227.4					
Second	1290.9		616		361.3		207.1		738.49		382.9		1037.1		468.0		910	358
Third	1911.4	1558.2	1050.9	736.2	643.8	475.2	404.7	262.9	1941.5	1260.0	1086.3	521.3	1407.3	1205.2	888.5	565.3		
Fourth	2131.6	1526.4	1284.4	672.7	942.4	553.6	659.7	340.4	2547.8	1329.9	1407.9	579.4	1546.4	1560.2	941.1	538.2		

[1] Series A, upper line represents upper part and lower line the lower part of plant.
[2] Series C, upper line represents petioles and midribs, lower line true stems.
[3] Series C and D, upper lines represent underground stems, lower ones stolons.

absorbed also increased. Their data plotted against time show that in the later stages there was a slightly lower rate of dry-matter accumulation and of intake of nitrogen, phosphorus, and potassium by the total plant but that the intake by tubers continued in practically a straight line; that is, the tubers continued to absorb minerals at the same average rate each day but they absorbed some of these and perhaps some organic matter from the plant tops, in which the amount decreased during the last period. They found no evidence that any of the nutrients returned to the soil. Berkner (*11b*) reported that the demand of the plant for N was exceeded only by that for K and that to a large degree the N intake governs the increase in dry matter. He found it to be taken up by the plant till the conclusion of the vegetative period.

When the nitrogen requirements are being investigated it is desirable to know how much can be procured from the parent seed piece. Denny (*29*) found, in Triumph potatoes, that by the time plants were above ground with fully formed leaves 50 per cent of the total nitrogen had been removed from 14-gram seed pieces and 33 per cent from 56-gram pieces. The plants continued to absorb nitrogen during most or all of their period of existence. Plants 10 inches high with well-developed tubers had removed 83 per cent of the nitrogen from the 14-gram and 75 per cent from the 56-gram seed pieces. By the time they were in bloom they had removed 83.1 per cent from the 56-gram seed pieces. By the time tubers were forming the plants had removed 50 milligrams of nitrogen from small seed pieces, compared with 180 from the larger ones. Nitrogen was not removed as rapidly from Irish Cobbler seed pieces. Starch was removed even more quickly and completely than was nitrogen.

For the purpose of determining in this investigation when nitrogen was assimilated, the total amount of assimilated nitrogen in the plant at the time of maturity was considered as 100 per cent. The greatest percentage of the nitrogen was assimilated by the tops during the second period. In the tubers the greatest percentage of assimilated nitrogen was found during the third and fourth periods. When total amounts assimilated, Series A, B, and C,[7] on each date are plotted as percentages against time the rates of assimilation for the continual-nitrogen plants in each series were after all very similar (Fig. 28).

The shorter days diminished the percentage of the final total nitrogen which was assimilated during the later per-

[7] Series D data were not plotted because of the premature death of the plants.

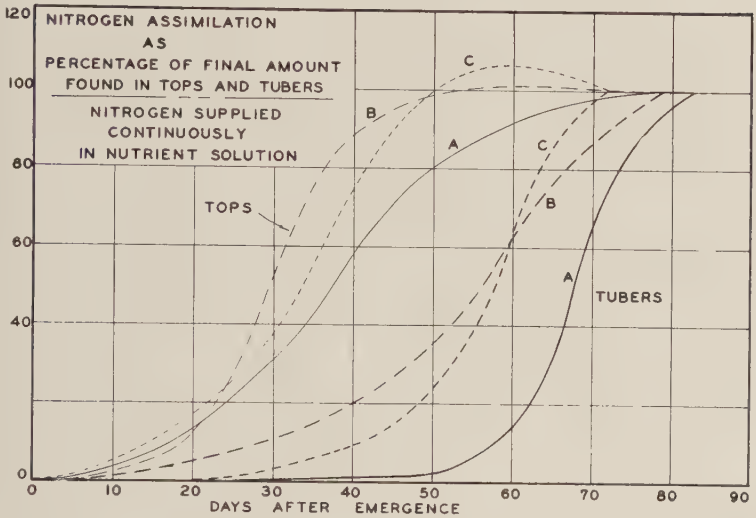


FIG. 28.—Percentage that the total amount of assimilated nitrogen per plant at the close of each period was of the final total amount in the plant at the close of the fourth period, for plants from each nitrogen treatment in each series. (Based on data in Table 24.)

iods in Series A and B, and decreased the top growth while the longer days of Series C increased these percentages during these periods and increased the top growth. The effect of withholding nitrogen upon the content of assimilated nitrogen in tops and tubers is graphically shown in Figure 27. The waves of nitrogen absorption reported as correlated with blooming aud tuberization (*68*) were not apparent in these series.

Rate of assimilation of ammonium and nitrate nitrogen.—The amount of nitrogen assimilated daily per plant (that is, transformed to organic forms) was greatest in the long-day, highest-temperature plants (D first, A second) and least in the shortest-day, low-temperature plants (B and C, Table 25). With short, warm days (DS) more was assimilated than with cool, short days. As days became warmer and longer the amount of nitrogen assimilated daily became greater (D) [8] but as they became cooler and shorter (A) the daily amount assimilated remained almost constant during the

[8] In view of the amount of burning of leaves by heat during the first few days of the third period, it is assumed that the weight of nitrogen assimilated daily would have been sufficiently higher than the amounts recorded, to constitute an increasing rate.

TABLE 25.—*Mean daily increase in amount of assimilated nitrogen found in the entire plant and in tubers during each period.*

Period	Series A 80° to 76° F. 14.5 to 12 hours				Series B 70° to 62° F. 10.8 to 9.2 hours				Series C 60° to 64° F. 10 to 13.3 hours				Series D 72° to 92° F. 14 to 15 hours			
(a) MEAN DAILY INCREASE IN ASSIMILATED NITROGEN (IN MILLIGRAMS) IN ENTIRE PLANT DURING EACH PERIOD																
First	11.9 [1]				3.9 [1]				6.3 [1]				15.2 [1]			
Second	36.1		12.1		14.6		6.5		30.5		13.1		54.0		16.0	
Third	33.5	14.4	23.5	6.5	14.5	5.8	10.1	2.9	44.1	11.6	33.5	6.5	39.0	17.7	44.3	10.3
Fourth	18.8	−2.3	16.7	−4.5	13.6	3.6	11.6	3.5	46.7	5.4	24.8	4.5	42.6	101.5	15.0	−7.7
(b) MEAN DAILY INCREASE IN ASSIMILATED NITROGEN IN TUBERS OF EACH PLANT DURING EACH PERIOD (IN MGS.)																
First	0				0.3				0				0			
Second	0.5		1.8		5.1		3.8		6.7		6.0		0.1		1.2	
Third	17.4	17.4	7.2	7.0	12.0	7.9	7.6	3.9	42.1	26.8	23.1	9.1	5.5	4.2	13.7	10.1
Fourth	16.3	7.1	12.2	2.3	13.7	6.0	10.7	4.0	49.2	18.8	25.6	7.6	−2.7	−5.6	−7.0	0.2
(c) PERCENTAGE THAT MEAN DAILY INCREASE OF ASSIMILATED NITROGEN IN TUBERS WAS OF TOTAL PLANT INCREASE																
First	0				7.1				0				0			
Second	1.4		14.9		34.9		58.5		22.0		45.8		0.02		7.5	
Third	51.9	120.9	30.7	107.7	82.8	136.4	68.2	135.0	95.5	231.0	69.0	149.0	14.1	23.7	31.0	98.1
Fourth	86.7	408.5	73.0	151.2	101.0	166.6	92.2	114.3	105.3	348.0	103.5	169.0	Tubers lost nitrogen			

[1] Figures for first period include any nitrogen which may have been translocated from seed pieces. Much of this occurred before sprouts emerged above the surface of the sand. Minus sign indicates that nitrogen was lost by plants or tubers. Data for various lots arranged as in previous tables.

second and third periods but then decreased rapidly. At low temperatures the daily increments of nitrogen assimilated were practically constant for Series B after the first period, whereas in Series C with days increasing in length the daily increment became greater up to the termination of the series. Thus it is evident that increases in either day length or temperature brought about increased nitrogen assimilation and that both together brought on still greater daily increments. The 50 to 75 milligrams of assimilated nitrogen that can be assumed to have been derived from the parent seed piece (*29*) would about account for the equivalent of the nitrogen assimilated by plants of Series B during the first period. This seed-borne nitrogen undoubtedly was an important factor in the entire period of growth of the short-day plants.

With the long, warm days almost all of the nitrogen assimilation was in the vegetative parts, and most of it was found in the leaves. With short days or low temperatures a considerable percentage of the nitrogen was allocated within the developing tubers. The slowing down or almost complete cessation of top growth in the short-day plants occurred during the period when tuberization was becoming the major activity of the plant (in so far as the building of dry matter was concerned). In Series B, 56.7 per cent of the nitrogen assimilated during the second period was found within the tubers.

In view of the conclusions from recent investigations the question is raised whether nitrogen was assimilated within the tubers (*90*). As plants became older the assimilated nitrogen within the tubers constituted a rapidly increasing percentage of the total amount, until as in Series C the daily increase in assimilated N in the tubers was 5.3 per cent in excess of the increase of the N assimilated by the entire plant, all portions of the vegetative parts having lost a small amount of assimilated nitrogen during the fourth period. With long, warm days the amount of nitrogen in the tubers was a very small portion of the amount in the plant. As days became shorter and cooler, tuberization finally constituted a major part of the activity in Series A with 51.9 per cent of the total nitrogen assimilation occurring within the tubers and increasing to 86.7 per cent during the fourth period. When days were warm, long, and increasing in length and when tuberization began about the 27th day after emergence, about 14.1 per cent of the nitrogen assimilated by the plant between the 30th and 39th days was in the tubers. However, during the period of excessive heat in early June the nitrogen assimilation was so very rapid in the tops that both carbo-

hydrates and nitrogen were translocated from the tubers, which decreased in total weight.

Withholding nitrogen from the nutrient solution at the close of the first period has been shown to have been a great stimulus to initiate tuberization with the long, warm days (A, D), to a slight degree with medium-length, cool days (C) and of little consequence with short days, regardless of temperature (B, DS, ES) because with the latter tuberization was already under way and very limited protein synthesis caused top growth to be slow. The withholding of an external nitrogen supply immediately diverted nitrogen away from the tops to the tubers somewhat in proportion to the extent that tuberization was initiated. The percentage going into tubers during the second period was approximately 35 times greater for the minus-nitrogen than for the plus-nitrogen plants in Series D, 10 times greater with Series A, but only twice as great with C and only a trifle greater with B. However, during the third period the tops were losing nitrogen and then because of the very rapid rate of tuberization in Series B and C, the small amount of nitrogen in their tops was rapidly withdrawn. The performance of the minus-nitrogen plants in Series D was very unusual, because the tubers retained their nitrogen or perhaps added some during the periods when nitrogen was lost from the top, whereas when nitrogen was being supplied the plant tops were taking nitrogen out of the tubers.

Nitrogen withdrawal at the end of the second period resulted, during the third period, in practically a complete cessation in elongation in stems of B and a less severe check in C, while with A there was still considerable elongation and in D elongation may have been accelerated. The gain in dry matter followed similar trends. With plants of this size and with tuberization well under way, total nitrogen assimilation was greatly reduced. There was no addition of assimilated nitrogen in the tops during the third period, except in 4D where it continued at a reduced rate with mean temperature at 92° F. In the fourth period at a lower mean of 85° F much nitrogen was assimilated in the tops. The validity of this very anomalous situation might be suspected, and the possibility of some experimental error should not be ignored, but the relative condition as compared with continued-nitrogen plants can be understood partially by remembering that the leaves of plants from which nitrogen had been withdrawn survived the few lethally high temperature periods better than did those of plants receiving nitrogen at the time. The minus-N plants were higher in carbohydrates, and were com-

parable to the minus-N plants of the tomatoes grown at 95° F. by Nightingale (*92*). The larger tops, developed because nitrogen had been available for a longer time before it was withdrawn, contained a large amount of mobile inorganic nitrogen and much organic nitrogen that could be hydrolyzed and translocated. The increase in both the volume and dry matter of the tops was made without assimilation of additional nitrogen; in fact it was made as the tops were actually losing nitrogen to the tubers. Although the tubers were assimilating a relatively small amount of nitrogen per day, most of it apparently had previously been assimilated in the tops. This translocation was responsible for the premature and frequently rapid senility of the lower leaves of these plants. Again Series D was an exception, the tops gaining in nitrogen as the tubers lost it.

When nitrogen was supplied to minus-N plants at the end of the second period, assimilation of nitrogen was greatly accelerated at once. The daily increment in nitrogen assimilated by the tubers was greater than where nitrogen starvation was continued. With short days and low temperatures a higher percentage of the total amount assimilated by the plant went into the tubers than with the long, warm days of D and A. In all series except D the percentages of the total amount of nitrogen assimilated daily by the tops were greater than where nitrogen was supplied continuously. As the nitrogen supply was continued the daily increment for the entire plant declined during the fourth period (except in Series B where plants were less mature), but then the percentage going into the tubers increased.

CARBOHYDRATE ASSIMILATION

Literature review.—Studying the composition of the potato plant as it developed, Rosa (*102*) reported reducing sugars to be low but quite constant in all parts of the plant except the underground stem, where they were high at emergence time but decreased rapidly until tuberization, when they again increased slightly. Sucrose was found to increase in leaves and aerial stems when stolons and tubers were developing. In underground stems it followed the same trend as reducing sugars but increased more at tuberization time. Starch was low at first and remained low in stems but increased in underground stems and leaves from emergence time on. There is general agreement that starch comprises a higher percentage of the leaf weight most of the time than either of the sugars (*22, 18, 10*).

The carbohydrate content and fractions varied greatly from hour to hour, being very sensitive to light and temperature changes, thus probably accounting for some of the conflicting statements. In the more recent work the opinion is held that glucose is the first sugar formed (*22, 10*) and that sucrose is the transportation sugar (*10, 10a*). Reducing sugars have generally been found at a minimum in early morning, increasing to a midday maximum, followed by a decrease and then another late-afternoon or early-evening peak, followed by a more or less steady decrease (*25, 22, 23*).

Sucrose varied during the day about as much as reducing sugars (*25, 22*) but was generally less abundant (*23*). It seemed always to be abundant in leaves when tuber formation began (*25, 102, 22*). Under controlled conditions Bushnell (*18*) reported, for large plants, a higher content of reducing sugars than sucrose in leaves and stems, with greatest over-night reductions in the sucrose percentages. Its increased abundance in the stems at tuberization time (*22, 102, 10*) and the gradient from midrib to lower stem (*10*) harmonize with the idea of its being the transportation sugar.

Clements (*22*) during long summer days with a diurnal temperature range of 8° to 30° C., reported lowest percentages of starch after midnight with a minimum generally at 8:00 A. M. The percentage then increased to a maximum in the late afternoon, though generally (depending largely upon light intensity) an almost equally high or higher point was attained in midday. Davis and Sawyer (*25*) reported starch maximum at two hours before sunset but Bushnell (*18*), calculating from their figures, reports an increase in starch content of stems during the night but his own work (*18*, pp. 22-23) showed a decrease in polysaccharides over night.

Improved illumination in the greenhouse increased the carbohydrate content of potato plants growing in incubators (*18*). Sucrose was found to be more abundant in a dry, warm season than in a cool, moist season (*22*). Fertilization practice was reported (*23*) as not causing significant differences in sugar content, but Hartwell observed pronounced starch accumulation when essential elements were deficient (*48*).

The loss of carbohydrates over night from the leaves of field plants was figured at 20.9 per cent and from stems at 7.7 per cent by Davis and Sawyer (*25*), but from incubator plants at different temperatures it was figured at from 42.1 to 54.7 per cent from leaves and 12.8 to 32.4 per cent from stems by Bushnell (*18*). The loss due to respiration and

translocation was greater at 20° C. than at 29° C. Of the amount lost from leaves the percentage not respired over night amounted to 46.5 at 20° C. and only 6 per cent at 29° C. (*18*).

Wilfarth, Romer, and Wimmer (*136*) and recently Smith (*111*) reported increased starch content in potatoes as the tuber size increased and as harvesting was delayed. Appleman and Miller (*5*) reported that reducing sugars and sucrose decreased while starch increased in the tubers until about 80 per cent of the leaves were dead. Sucrose was always more abundant than reducing sugars but relatively more so when tubers were making their most rapid growth. Smith (*113*) found that tubers produced with a soil pH of 5.64 to 6.05 had the highest percentage of starch, those produced at 7.16 to 7.45 had the lowest, and those at 4.68 to 4.90 were intermediate in starch content.

Renski (*100*) reported a distinctly higher percentage of starch in spheroidal compared with flat tubers. In the potato tubers Willaman and West (*137*) found dry matter to be correlated with specific gravity, but they did not find starch so correlated. They found carbohydrates were generally lowest in tubers grown in southern Minnesota. Tubers from sandy soils had the least dry matter, and from clay soils the least nitrogen. Goldthwaite (*44*) found that the percentage of starch and carbohydrates increased as potatoes were grown at higher altitudes. When the number of irrigations was increased so that the first irrigation was earlier and tubers were thus set on earlier, the starch content was increased. Weigert and Stiehr (*129*) found a greatly increased total carbohydrate content when potatoes were produced in nitrogen-deficient field plats as compared with nitrogen-fertilized or manured plats. Berkner and Schlimm (*11a*) reported a definite decrease in the starch content of tubers as applications of calcium nitrate were increased. This was accompanied by a decrease in the ratio of starch to protein.

Hydrolyzable polysaccharides other than starch were found to occur in all parts of the plant generally more constantly but less abundantly than starch. Clements (*22*), considering these under the term hemicellulose, thought them to be reserves used when other forms were practically consumed. He suggests that when carbohydrates are formed rapidly they (hemiculluloses) act like starch; but when starch is being formed with sufficient rapidity to remove the sugars from the chloroplastid solution the sugars do not diffuse in large quan-

tities into the vacuole of the cell where sucrose is apparently formed. When sucrose accumlates in excess concentration, hemicellulose is formed to remove it from solution. In a favorable year for potato production, hemicellulose fluctuated greatly, apparently functioning as a temporary reserve; but in a less favorable year, when it was more constant, it appeared to be a water holder, for as the percentage increased the leaves wilted less during a drouth period.

Results from macrochemical analyses.—The plants of Series 2C which were tuberizing rapidly had a lower percentage of all carbohydrates, in all parts except tubers which had more of all except sucrose, than did the more vegetative plants of Series 2A (Tables 26 and 27). This might indicate that the tubers were able to absorb the carbohydrates as rapidly as they were transported in Series C but that in Series A there

TABLE 26.—*Carbohydrates in various plant parts as percentage of dry weight.*

Lot No. and N nutrition in prior periods [1]	Series A—Long and warm days						Series C—Short to intermediate length and cool days		
	Leaves		Stems			Tubers	Leaves	Stems	Tubers
	Upper	Lower	Upper	Lower	Subt [2]				
REDUCING SUGARS									
1 +	0.67		1.05		1.53				
2 ++	2.08	1.49	4.94	3.44	0.85	2.11	1.00	3.27	0.94
5 +0	1.42	1.29	3.51	2.03	0.87	0.94	1.27	3.04	1.02
3 +++	2.08						1.83		
4 ++0	3.14						2.18		
7 +00	4.22						1.72		
6 +0+	2.65						1.99		
SUCROSE									
1 +	1.04		0.98		0.29				
2 ++	2.33	2.23	2.10	2.00	1.65	6.07	2.51	0.51	12.10
5 +0	3.94	2.32	2.33	2.90	3.07	7.99	2.83	1.81	10.52
3 +++	2.62						4.11		
4 ++0	4.40						4.68		
7 +00	4.21						4.04		
6 +0+	3.97						3.73		
STARCH AND DEXTRIN									
1 +	3.68		2.60		0.79				
2 ++	4.78	2.71	2.73	3.15	5.59	40.10	5.05	2.82	34.78
5 +0	9.48	2.93	2.38	4.30	6.92	46.90	6.78	2.94	44.72
3 +++	2.49								
4 ++0	2.47								
7 +00	1.25								
6 +0+	3.11								
ACID HYDROLYZABLE POLYSACCHARIDES (NOT STARCH OR DEXTRIN)									
1 +	1.95		3.65		5.31				
2 ++	2.26	2.54	5.27	7.38	6.94	3.57	3.14	4.21	5.74
5 +0	3.04	2.80	5.73	6.74	7.78	5.03	3.07	5.17	7.52
NON-HYDROLYZABLE RESIDUE									
1 +	22.2		24.4		38.7				
2 ++	24.2	23.4	32.9	37.7	36.2	6.90	26.2	24.2	5.00
5 +0	21.3	22.3	29.2	36.0	36.2	7.50	26.5	29.4	3.60

[1] The sign + indicates that N was supplied in nutrient solution, 0 that it was omitted. Position of sign indicates N treatment during first, second, or third periods respectively.

[2] "Subt" indicates subterranean stems, *i.e.*, underground stems and stolons.

TABLE 27.—*Carbohydrates in various plant parts as percentage of fresh weight.*

Lot No. and N nutrition in prior periods [1]	Series A—Long and warm days						Series C—Short to intermediate, cool days		
	Leaves		Stems						
	Upper	Lower	Upper	Lower	Subt [2]	Tubers	Leaves	Stems	Tubers
REDUCING SUGARS									
1 +	0.072		0.060		0.125	0			
2 ++	0.264	0.159	0.337	0.255	0.108	0.233	0.105	0.165	0.118
5 + 0	0.188	0.166	0.244	0.159	0.121	0.121	0.119	0.168	0.153
3 +++	0.294						0.192		
4 ++ 0	0.546						0.205		
7 + 00	0.978						0.155		
6 + 0 +	0.380						0.195		
SUCROSE									
1 +	0.111		0.056		0.024	0			
2 ++	0.296	0.238	0.143	0.148	0.210	0.670	0.262	0.026	1.607
5 + 0	0.522	0.298	0.162	0.227	0.428	1.021	0.265	0.100	1.573
3 +++	0.370						0.430		
4 ++ 0	0.764						0.443		
7 + 00	0.976						0.364		
6 + 0 +	0.570						0.366		
STARCH AND DEXTRIN									
1 +	0.393		0.148		0.065	0			
2 ++	0.606	0.289	0.186	0.234	0.710	4.430	0.526	0.142	4.620
5 + 0	1.256	0.377	0.166	0.337	0.964	6.010	0.635	0.162	6.700
3 +++	0.352								
4 ++ 0	0.764								
7 + 00	0.290								
6 + 0 +	0.446								
ACID HYDROLYZABLE POLYSACCHARIDES (NOT STARCH OR DEXTRIN)									
1 +	0.208		0.208		0.435	0			
2 ++	0.287	0.271	0.360	0.547	0.882	0.395	0.328	0.212	0.762
5 + 0	0.403	0.360	0.398	0.528	1.084	0.644	0.288	0.285	1.126
NON-HYDROLYZABLE RESIDUE									
1 +	2.370		1.392		3.167	0			
2 ++	3.068	2.492	2.248	2.792	4.595	0.761	2.74	1.218	0.664
5 + 0	2.822	2.870	2.030	2.822	5.042	0.961	2.48	1.620	0.539

[1] The sign + indicates that N was supplied in nutrient solution, 0 that it was omitted. Position of sign indicates N treatment during first, second, or third periods respectively.

[2] "Subt" indicates subterranean stems, *i.e.*, underground stems and stolons.

was congestion in the stems because tuber development was not sufficiently advanced, being still in the meristematic stage to a greater degree, as shown by the higher percentage of reducing sugars and assimilated nitrogen and lower percentage of inorganic nitrogen (Tables 20 to 23). The high percentage of sucrose in C was possibly due to sucrose being absorbed more rapidly than it could be converted into starch. This more rapid absorption may have been possible because of the greater content of acid-hydrolyzable polysaccharides other than starch or so-called hemicelluloses (*22*). These compounds by developing more colloidal imbibition force may have made possible the absorption of a more concentrated sucrose solution. In turn the higher hemicellulose content may have been the result of a higher sucrose content when the tuber could not take the starch out of solution with suf-

ficient rapidity (*22*). The slightly higher amount of polysaccharides in the leaves of C may indicate slightly greater accumulation of carbohydrates because of a lower respiration rate.

Withholding nitrogen during the second period brought about a general increase in all carbohydrates except reducing sugars in all parts of the plants (5A and 5C compared with 2A and 2C). The sucrose content was not increased in the tubers of 5C but the starch content was increased greatly. During this period the tuberization rate was increased about seven times in A but only one-half in C, by withholding nitrogen. According to microchemical observations made during the period, starch congestion at the end of the second period was still increasing in the stems of 5A because of lessened growth, but was decreasing in 5C, though still greater than in 2C. Thus at the time of sampling, carbohydrates were coming into the tubers at a decreasing rate instead of an accelerated rate (when figured as a percentage of the previous tuber weight or on a logarithimic basis as calculated by James (*51*). Furthermore these tubers whose growth had been stimulated early in the period were now larger and less meristematic (shown also by reduced percentage of assimilated nitrogen), than some days earlier or than those of the continual-nitrogen plants (2C). They probably had developed a greater capacity to assimilate carbohydrates. The greater percentage of carbohydrates in the stems resulted mostly from sucrose increase. Very plausibly this might have been due to the greater concentration of the solution because of more carbohydrates being transported without an increase in the capacity of the transportation system.

The tubers of the nitrogen-starved plants of the short-day, low-temperature series had the highest percentage of all carbohydrates, but the tops were different. These plants were declining in vigor and their leaves were pale and less active photosynthetically (Table 5a). In 5A the top leaves were relatively new and vigorous and the older, lower leaves were more comparable to those of 5C. As a consequence the younger tubers of 5A did not take in all the carbohydrates, and increased congestion occurred throughout the system.

When plants were producing stolons actively but not yet forming any tubers (1A), glucose increased from top to bottom in the stem but all other carbohydrates decreased. After this initial period of very rapid stolon growth, there followed the period of very active top growth and very little tuber growth (2nd period). The reducing sugars were highest in

the top stem and decreased downward, whereas all the other carbohydrates increased downward (2A). This downward increase of more complex carbohydrates was accentuated by elimination of the external nitrogen supply (5A). The reducing sugars were highest in regions of growth; the other carbohydrates were associated with the reserve accumulation. These results were apparently in accord with those of Rosa (*102*). It is of interest to note that when calculated on the dry-weight basis the sucrose gradient was not steep but was in the same direction as the glucose gradient of 2A. This might be a characteristic of the transition stage with the initiation of tuberization.

The acid hydrolyzable polysaccharides remaining after starch was removed were more prevalent in leaves and tubers of 1C than of 1A but less prevalent in stems. They generally increased in all parts of all plants after the external nitrogen supply was withheld. In almost every instance the percentages of acid hydrolyzable polysaccharides on the fresh basis followed the same trend as those for sucrose, as pointed out by Clements (*22*). They also followed the fluctuations of starch percentages, except in tubers. They were more prevalent than starch in stems, less in leaves, and very much less in tubers.

The increased carbohydrate content of tubers from low-nitrogen plants and short-day plants may be partly due to the larger size of those tubers, the difference being of about the magnitude reported for starch content of tubers of about the size ranges involved—mostly 1 to 50 grams (*136, 113*). However, Weigert and Stiehr (*129*) report greatly increased percentages of carbohydrates in tubers when grown on soils deficient in nitrogen.

Microchemical observations of starch accumulation.—In the plant cells starch is formed whenever sugar accumulates beyond the maximum amount that will remain in solution, although it has been suggested that hemicellulose is formed when the sugar concentration increases more rapidly than it can be converted into starch (*22*). This condition occurs in the cells because photosynthesis or movement of sugars from adjacent cells increases the sugar content beyond the needs of the cells or the ability of the cell to pass the sugar on to adjacent cells. Thus starch may occur in isolated cells or in groups of cells or in entire organs for either very brief or very extended periods, depending upon the adjustment of the plant to the situation or changes in the environment.

In the green and growing plant, whenever the surplus photosynthate is in excess of the transportation facilities,

starch accumulates relatively close to the active photosynthetic area—first in the leaves, then in the petioles and stems. If the storage organs are not capable of receiving the reserve as rapidly as it is transported, the congestion occurs in the stolons, moving inward to the stems and then up the stems toward the leaves. In such plants more starch is likely to be found in all parts and in greater amounts than where congestion is due only to the transportation system. In plants that are tuberizing rapidly the tubers may assimilate carbohydrates as rapidly as they are produced yet there will be an excess of starch in some part of the plant (and a different part) during practically every hour of the day.

Hartwell (*48*) found that starch congestion increased when the supply of some essential mineral nutrient was deficient. Congestion was generally greatest in the basal portions when samples were taken early in the morning.

In a study made during mid-November, 1932, during sunny days with plants that were receiving nitrogen and were tuberizing rapidly, the starch content of the various sections of the stem was found to vary considerably at different hours of the day. In the lower stem it decreased from a very large amount at 9:00 A. M. to practically none at 4:30 and 7:00 P. M., increased to a small amount at midnight, and again increased to a very large amount at 9:00 A. M. In the underground stem starch was found in exceedingly large amounts at 9:00 A. M., but none was found at any other time of the day. With plants showing much greater starch congestion because of having been without nitrogen for ten days, starch never disappeared entirely from these various stem portions but the amount in each fluctuated in the same order as in the plus-nitrogen plants.

The appearance or disappearance of starch from the stems was found to be a good indicator of any change in physiological tendencies. The changes in starch accumulation could be observed earlier and with greater certainty than changes in growth rate, leaf color, or other changes externally visible.

The microchemical observations for starch were reduced to comparative basis by estimating the prevalence of starch, on a 1-to-10 basis, in sections taken at different levels and from these arriving at a general value for the entire stem length. The samples were secured about three hours before sundown during bright days at intervals appropriate to the changes which were occurring. Although such a method cannot be considered exact, it serves very well to depict a response which occured under different light and temperature

conditions when the external nitrogen supply was changed. The data are presented in a series of smoothed curves in Fig. 29.

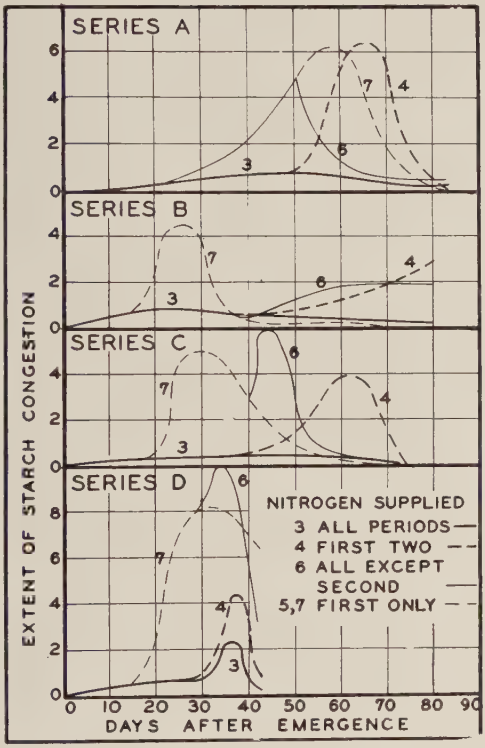


FIG. 29.—Relative amount of starch accumulation at various times in the stems of the plants receiving different nitrogen treatments in each series.

With a continual nitrogen supply in all plants there was generally a small amount of starch throughout the endodermis at the time the sprouts emerged but this disappeared almost entirely when leaves appeared. Little starch was thus found during the first few weeks after emergence except at the very base of the stem next to the old seed piece and just behind the stem and stolon pieces. (Leaves were not studied microchemically.) Throughout their existence relatively little starch was seen in stems of plants continuously supplied with nitrogen.

When nitrogen was withheld at the end of the first period, starch accumulated at an accelerated rate because carbohydrates were not used in protein synthesis. A slight increase was noticed in seven hours and a distinct increase was apparent within two days. This accumulation increased steadily to a maximum amount many times greater than that of the continual-nitrogen plants (Fig. 29). After that it decreased rapidly till very little was visible, and finally, when the plants were almost dead, practically none was seen.

These starch increases were the result of reduced demands for carbohydrates for growth. As nitrogen became less available and the growth rate diminished, the amount of starch increased. The turning point in the starch content came

about as a result of the break-down of the chlorophyll and chloroplasts and later death of the leaves when nitrogen was so completely exhausted that the chlorophyll supply could not be maintained or the nitrogen was passing from the tops into the tubers. With the amount of photosynthate thus inevitably reduced, all of it and a little more could be assimilated by the tubers, until finally the stems were cleared of starch (Figs. 29 and 30). Still later more carbohydrates were translocated than were manufactured daily. The first starch deposition occurred in the endodermis, after which it was most likely to be found in the inner cortical cells, then almost simultaneously in the parenchyma of the pericycle and that adjacent to the outer and inner phloem, then in the Markkrone (9) or parenchyma that might be considered either xylem or inner phloem, then in the outer pith, the central pith, and finally in the medullary rays through the xylem. When starch disappeared the order was reversed. Most of the starch disappeared from cells inside the cambium before very much was taken out of the cortex.

When the volume of the stems and stolons was small in proportion to the total leaf volume as in Series B, the space available for temporary storage (cortex and pith) was also greatly reduced. Then when the amount of reserve carbohydrates was increased by reducing growth, the starch congestion was more apparent than if the stem had had a greater area, even though there was only a slight increase in carbohydrate as a result of a slight reduction. This is probably why the congestion appeared to be most rapid in Series B. In Series C the congestion was not so early, because more of its carbohydrates continued to be used in growth, which was more prolonged after nitrogen was withheld than in B, but finally when growth practically ceased the congestion was greater. When days were long and warm (Series A), the stems and stolons being very thick, the leaf/stem ratio was low; and, growth having continued for a considerable time after nitrogen was withheld, starch accumulation was a more gradual but more extensive process than in the short-day, low-temperature plants. The more rapid disappearance of this accumulated starch might have been due to the much higher respiration rate at the higher temperature. With long days of medium temperature (D) growth was very active for ten days following nitrogen withdrawal, but then, when the supply of N available for protein synthesis was exhausted, starch accumulated with extreme rapidity and density throughout the entire stem in spite of increasing temperatures (Fig. 31). The stolons were very thick, increasing

in thickness from base to tip. In those stolons growing toward the surface this tapering thickening did not occur and the apical inch was almost devoid of starch. Several things may have contributed to this very great accumulation of starch, when respiration was very high. The reduced growth rate not only made more carbohydrates available for reserve but it also brought about a "hardening" process and a more xeromorphic condition such as thicker cuticle, heavier walls, etc., which enabled the leaves to survive this period of excessive heat when leaves of high-nitrogen plants wilted and burned—and thereby maintained a relatively greater photosynthetically active leaf surface. Possibly, therefore, more

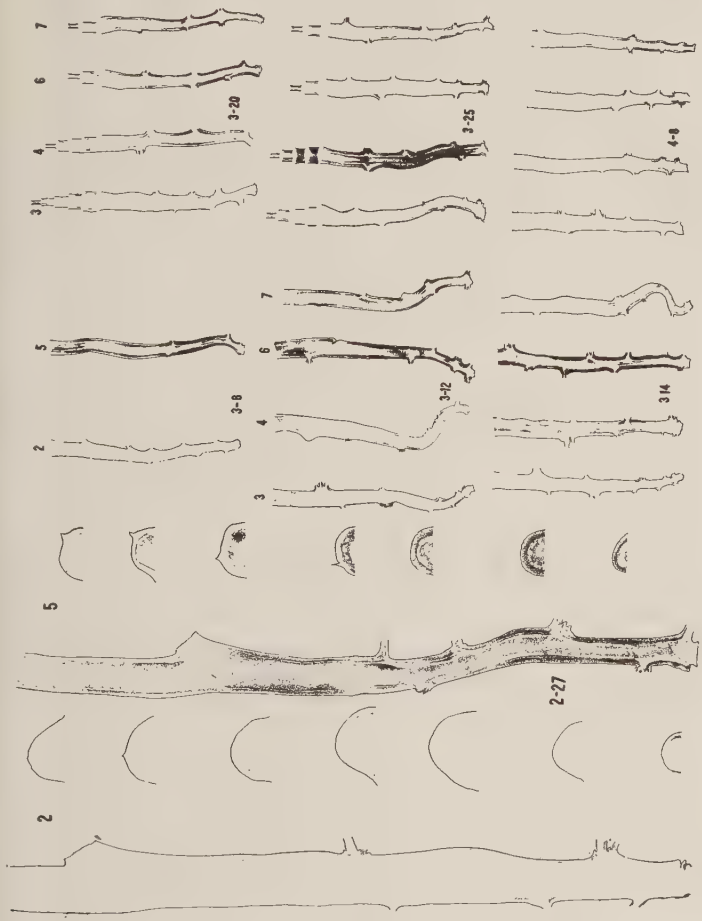


FIG. 30.—Starch in stems of Series C. Numbers at top are nitrogen treatment numbers; those between are dates harvested. Lower halves of 2 and 5 at left are underground portions. The transverse sections of 2-27 were taken from the portions of the stem located at the level of the straight edge of the sectional sketches. The small segments at the top of 3-20 and 3-25 depict starch at successive levels (10 cm.) in the aerial stems. Underground-stem portions shown were approximately 10 cm. long. (For tuber production by these plants, see Fig. 19; for tops, Fig. 4.)

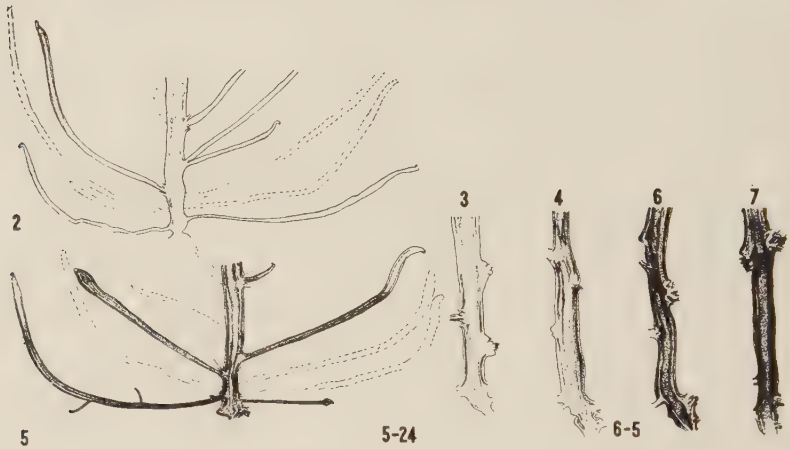


FIG. 31.—Starch accumulation at two periods in the underground portions of plants receiving different nitrogen treatments in Series D. In Lot 5 starch was scarce near tips of stolons, the tops of which were being converted into leaf-bearing shoots. Withholding nitrogen for six days (June 5) resulted in an easily perceptible increase in the accumulation of starch in the underground stem (Lot 4 compared with Lot 3) but its addition to N-deficient plants resulted in a barely discernible decrease (Lot 5 compared with Lot 7). (For tuber production by these plants. see Figure 20, and for plant tops, see Figure 5.)

carbohydrates were being manufactured and quite evidently less were being used. These underlying causes enabled this set of plants to produce the maximum crop of tubers at the end of the 52nd day. Much of the daily tuber gain, occurring when those of other treatments were losing weight, came from the accumulated starch in the extensive parenchyma of the stolons and stems. Practically all of this starch had been removed when the series was terminated.

Changing the nutrient solution to minus nitrogen at the beginning of the third period brought about the same type of starch accumulation as did early nitrogen withdrawal. In plants that were still making considerable growth (A, C, D) the accumulation was more rapid but to about the same relative extent. When plants were not growing (B) the increase in starch accumulation was relatively slow. In this series the surplus nitrogen held in the tissues of the plant enabled it to maintain a more adequate chlorophyll supply for a longer time.

Supplying nitrogen to N-deficient plants sometimes increased and sometimes decreased the starch accumulation. Increases were brought about by virtue of restoration of the chlorophyll and protoplasm in general. The leaves became

greener and the photoplasm appeared less hyaline within the first two or three days. There was an immediate response in increased carbohydrate manufacture, and starch accumulation resulted for a period (Fig. 30). Accumulation was reduced rapidly by activation of growth of tubers, so that they could assimilate carbohydrates more rapidly, and by reduction of reserve through renewed growth of tops (latter not applicable in B where response was least of any series).

In Series A with medium-length, warm days the reserve starch was depleted rapidly because of rapid respiration and the immediate top growth initiated when nitrogen was available. The previously initiated tubers were able to store all the reserves that accumulated from these new leaves, hence congestion was no greater than in continual-nitrogen plants. In Series D with nitrogen addition there was an initial increase in starch in stems already severely congested. This was probably due to the rapid improvement of the photosynthetic machinery before growth was sufficiently under way to require much carbohydrate material. Accompanying or immediately following this extreme accumulation, tuberization was accelerated, but the succulent new growth that followed caused not only all of the reserve starch in the stems but also that in the tubers to be used up by the tops. This process was already under way on the sixth day when sections sketched in Figure 31 were obtained.

DISCUSSION AND CONCLUSIONS

A. *Potato plants grown with an abundant available nitrogen supply* under conditions favorable for carbohydrate synthesis were found to have been:

1. *Vigorously vegetative but producing no tubers* (or at least very small amounts of tubers very slowly), when respiration and the synthesis of nitrogen compounds for new growth consumed all carbohydrates that were elaborated. Such conditions occurred with long, warm days in the early life of plants of Series A and D. Such plants were found to be relatively low in dry matter, sugars, polysaccharides and inorganic nitrogen, but high in moisture and assimilated nitrogen. The ratio of leaves to stems was relatively low. Stolons were numerous, thick, long, and much branched; many of them came to the surface and produced leaves.

With a continual nitrogen supply in all plants there was generally a small amount of starch throughout the endodermis at the time the sprouts emerged but this disappeared almost entirely when leaves appeared. Little starch was thus found during the first few weeks after emergence except at the very base of the stem next to the old seed piece and just behind

the stem and stolon pieces. (Leaves were not studied microchemically.) Throughout their existence relatively little starch was seen in stems of plants continuously supplied with nitrogen.

When nitrogen was withheld at the end of the first period, starch accumulated at an accelerated rate because carbohydrates were not used in protein synthesis. A slight increase was noticed in seven hours and a distinct increase was apparent within two days. This accumulation increased steadily to a maximum amount many times greater than that of the continual-nitrogen plants (Fig. 29). After that it decreased rapidly till very little was visible, and finally, when the plants were almost dead, practically none was seen.

2. *Weakly vegetative and not producing tubers,* when respiration was so high that all carbohydrates were used up about as fast as they were synthesized, leaving little or none for new growth, and even complex nitrogen compounds previously formed were broken down in order to procure additional carbohydrates for respiration. Such conditions occurred during the very long hot days with Series E and latter days of Series D (3′ D). Under such conditions the carbohydrates were resorbed from any tubers which may have been formed previously. Such plants were relatively high in dry matter and assimilated nitrogen but low in all carbohydrates and deficient in chlorophyll as shown by a pale color. Leaves were very small, as was the ratio of leaves to stems. Stolons were either not produced or were very weak. Under the more extreme conditions in Series E almost no supporting tissue was developed in the stems.

3. *Weakly vegetative but very succulent and very active in producing tubers* when conditions were not favorable for nitrogen assimilation by the tops but very favorable for carbohydrate synthesis. Such conditions occurred when the days were short and the temperature was low (Series B) and even when the temperature was high (Series DS and ES). These plants had very succulent tops and the percentage of dry matter in leaves and especially stems was very low, but the percentage in the tubers was very high. The percentage of inorganic nitrogen, especially nitrates, was continuously very high. The percentage of assimilated nitrogen was low in vegetative parts and high in tubers, if figured on the fresh-weight basis, and the reverse on the dry-weight basis. Microchemical tests revealed only a very small amount of starch in the stem, carbohydrates having been translocated quickly into tubers with almost complete clearance of starch from

stems over night. The leaves were very large and dark and leaflets few. The leaf/stem and top/tuber ratios were highest of any observed but because of small leaf area total weight of tubers per plant was less than with slightly more vegetative plants. Stolons were few and short. Tuberization was most active at the lower temperature because of a low rate of respiration and low nitrate assimilation.

4. *Mediumly vegetative, succulent, and very active in producing tubers* when conditions were very favorable for photosynthesis, and somewhat more favorable for nitrogen assimilation than in the previous classification. Such conditions occurred when days were short to intermediate in length (C) or long to intermediate (latter part of A). When compared with the more vegetative plants of Series A these plants had a lower percentage of dry matter and assimilated nitrogen in the tops, and less reducing sugar in all parts, less sucrose in stems and leaves, and less starch in stems, while on the other hand they generally had more inorganic nitrogen, more starch in leaves, and more sucrose, starch, and dry matter in the tubers. The low carbohydrate content was due to the adequate time and facilities available for their translocation and storage in the tubers where all forms were high except reducing sugars. The low percentage of hemicellulose and unhydrolyzed residue are the result of lack of differentiation of woody tissues. When compared with the less vegetative plants of B, they had a higher percentage of dry matter in all parts and also more assimilated nitrogen but slightly less inorganic nitrogen, while the starch content was about the same in both. These plants had large leaves and a high leaf/stem and tuber/top ratio, and they produced the greatest weight of tubers per plant.

B. *When the metabolism of the plant was altered by abruptly omitting nitrogen from the nutrient solution* the plants soon became weakly vegetative, less succulent, lower in inorganic and organic nitrogen, and higher in carbohydrates of all kinds (except perhaps reducing sugars) in all parts, and tuberization was either initiated or accelerated. The accumulation of carbohydrates was due to the inability of the plants to use them for synthesis of proteins and consequent new growth, since nitrogen was not available. They gradually disappeared from the stem, because of increased storage capacity in the developing tubers and decreased synthesis of the chloroplasts, which were deteriorating because of nitrogen deficiency in the nutrient solution or because of the actual translocation of nitrogen from tops to tubers. As a consequence of the inability to maintain an adequate chlorophyll

supply the tuberization rate was accelerated for only a brief period, after which it dropped below that of the plants receiving nitrogen and continued to decrease at a more rapid rate. In all series the withholding of nitrogen increased the ratio of dry weight of tubers to tops and decreased the ratio of leaves to stems.

The most extensive carbohydrate accumulation and relatively greatest acceleration of tuber development, as a result of nitrogen withdrawal, occurred in the most vegetative plants, which had not been tuberizing (Series A and D). The dry-matter content of all parts of these vegetative potato plants was increased by the nitrogen deficiency, thus probably accounting for the increased resistance of these plants to very high temperatures and their ability to increase the weight of their tubers when those on the nitrogen-supplied plants were being resorbed.

When plants were weakly vegetative, succulent, and non-tuber-bearing because of excessive respiration, the life of the plants was prolonged, because with nitrogen deficiency the carbohydrates were partially conserved but not sufficiently so to create a reserve sufficient for initiating tuberization. With plants that were weakly vegetative, succulent, and actively producing tubers (Series B) the withholding of nitrogen caused a decrease in dry-matter content of all parts except tubers, where it increased. Carbohydrates increased only slightly and tuberization was accelerated less than in any of the other series. In fact tuber production per plant was never greater during any period than where nitrogen was supplied continuously. When plants were slightly more vegetative and less succulent but still tuberizing very actively, the carbohydrates increased slightly and tuberization was accelerated slightly more than in the less vegetative and more succulent plants.

A deficiency of nitrogen at the time plants had almost attained their maximum vegetative growth resulted in practically the same type of responses as when the deficiency occurred earlier.

C. *When the metabolism of the plant was altered by abruptly supplying an abundance of nitrogen to plants that had not been receiving any during the second period,* the percentage of inorganic nitrogen was greatly increased while that of organic nitrogen was increased still more. In all parts the percentage was almost as great as in the plants that had received nitrogen continuously or sometimes even greater. The prompt change in the color of the leaves from a very pale, whitish green or yellow to a deep green color indicated that

the chlorophyll supply was re-established before growth was resumed. When environmental conditions were very favorable for nitrogen assimilation and new growth of tops, as in long, warm days, growth was resumed quickly with a consequent decrease in the previously high dry-matter and carbohydrate content of the plant and there was retardation of tuber growth. With the establishment of the new leaves there was again an increase in carbohydrates and tuberization. When conditions were less favorable for nitrogen assimilation and growth in top as at low temperatures and with short days, the small amount of new growth did not get under way for some time, but because of the prompt reinstatement of the chlorophyll supply and consequent increase in carbohydrate synthesis there was a slight increase in percentage of dry matter in leaves or even stems and a great increase in the carbohydrate percentage as well as a prompt acceleration of tuberization. During the third period (the first after N was resupplied) the tubers represented about 88 per cent of the total dry-weight increase with short, cool days but only 54 to 58 per cent with long, warm days.

With the resumption of growth and increased carbohydrate-absorption capacity of the tubers, these accumulated carbohydrates gradually disappeared from the vegetative tops. The dry-matter content of the tubers in all series was lowered at once upon the addition of nitrogen, and although it increased later it never was as great as where nitrogen was continuously supplied. The total final weight of tubers was increased by nitrogen reinstatement but never was as great as when nitrogen had been supplied continuously or when the nitrogen deficiency occurred later in the life of the plant. However, when respiration and growth demands were greatly increased by increased day length and temperature the addition of nitrogen to high-carbohydrate plants not only exhausted the carbohydrate content of the stems but also of the tubers, so that they decreased in weight even more rapidly than when nitrogen was continuously available.

The assimilated nitrogen in the tubers was increased in all instances, but the greatest increase and highest percentage occurred under the conditions least favorable for nitrogen assimilation by the leaves and stems. Under these latter conditions the tubers were also receiving a very much greater percentage of the nitrogen assimilated within the entire plant than was occurring when conditions were more favorable for vegetative growth.

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